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BY
H. C. GILSON

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THE LIFE HISTORY OF *ERPOBDELLA OCTOCULATA* (LINNAEUS, 1758)

BY K. H. MANN

Department of Zoology, The University of Reading

(With 4 Figures in the Text)

METHOD

The study was made in the Foudry brook, Mortimer, Berkshire (National Grid Reference 674644), in a reach which has a width of about 6 ft. and steep banks about 4 ft. high. During the summer months the depth of the water rarely exceeds 9 in. The stream drains an area of heath land, where plateau gravel rests on Bagshot beds and London Clay, and the water is only moderately hard (total alkalinity about 90 mg. $CaCO_3$/l.). The catchment area includes a good number of cottages, and the stream has a high content of dissolved organic matter.

The bed of the stream consists of a layer of coarse gravel, at the surface of which are large flints. When the volume of water passing down the stream is very small, there may be a deposit of fine silt on the stones, but for most of the year they are kept free from this deposit by the scouring action of the water.

This substratum seems ideally suited to the habits of *Erpobdella octoculata* (L.),* as large numbers of this species of leech were found on the stones whenever they were examined. As far as could be discovered during the investigation the leeches do not venture into the gravel beneath, nor into the banks, but spend the whole of the time on the stones, feeding on the organisms present there, and depositing their cocoons on the stones. It was discovered, in the course of collecting, that the leeches are seldom present on stones less than about 2 in. in diameter, probably because these are liable to be moved by the current. Accordingly, the method adopted for sampling the population was to examine all stones greater than 2 in. across, collecting every leech seen. The first sample showed that *E. octoculata* comprised 90% of the leeches present, the remaining 10% being made up of approximately equal numbers of *Glossiphonia complanata* (L.) and *Helobdella stagnalis* (L.). In order to study the breeding, growth and age of the leeches in the population, six samples were taken at intervals of approximately one month, between 29 April and 11 September 1952. At each sampling about 100 leeches were collected, weighed individually, and returned to the stream. Each sample was taken from the same stretch of water, and after weighing care was taken to distribute the leeches as evenly as possible over the collecting ground.

The routine used in weighing was devised to ensure that each leech carried over the minimum amount of water and that this amount was reasonably constant in

* The leech here referred to as *Erpobdella octoculata* (L.) is not the *Herpobdella octoculata* of Harding (1910) and others, but corresponds to Harding's *H. atomaria* Carena. For an explanation of this change see Mann (1952).

relation to the size of the leech. The leeches were placed in a shallow glass dish and left undisturbed for a few hours. Each in turn was then persuaded to loose its hold with its suckers, by gentle prodding with a seeker, and then lifted on to the weighing pan by placing the seeker under the middle of the body. Repeated weighings of the same leech showed that the amount of water carried over was sufficiently constant to enable the 'wet weight' to be accurately determined to the nearest 10 mg. If a leech was not caught on the seeker at the first or second attempt, it was left alone for some time, since *Erpobdella* secretes a copious amount of mucus when violently stimulated, and this seems to absorb water and increase the amount carried over.

For the first three months of the experiment a normal chemical balance was used for the weighing, but this proved extremely tedious, and a simple spring balance was constructed and used in July, August and September. The idea of using the balance

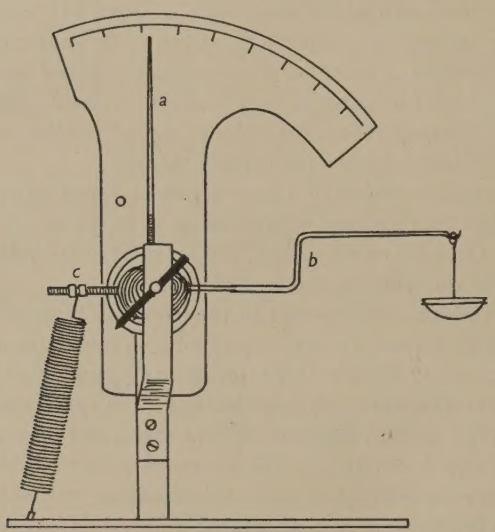

Fig. 1. Diagram of spring balance devised to facilitate direct weighing of live leeches. The fulcrum is the balance wheel of an alarm clock. Arm *a* bears a glass pointer; arm *b*, which is also of glass, supports a light plastic pan; arm *c* is threaded so that the moment of the main spring may be varied.

wheel of an alarm clock for the fulcrum was borrowed from Clarke (1952). As may be seen in Fig. 1, there are attached to the balance wheel three arms at right angles. Arm *a* bears the pointer, arm *b* supports the pan, and arm *c* is threaded to take two small nuts. Between these nuts is a connecting link for the main spring, which at its other end is attached to the base plate. The position of the two nuts may be altered when adjusting the total range of the instrument. The hair spring from the clock may be used to give zero adjustment. The scale is an arbitrary one which is calibrated on each occasion of use. It was designed so that each division corresponds to about 10 mg., thus ensuring that the leeches' weights could be read with confidence to the nearest 10 mg.

In order to obtain information about the density of the population and the number of cocoons deposited by each leech during the breeding season, a census was taken

on 30 May of the number of leeches and cocoons present on 300 stones. Subsequently, at short intervals of four to seven days, the number of cocoons present on 200 stones was recorded. On every occasion the census was taken on the same portion of the stream bed, an area of about 50 sq. yd.

Each time a sample of 100 leeches was weighed, two characters were recorded: (i) whether the clitellum was visible, and (ii) whether the vasa deferentia were visible through the ventral body wall, on account of their being distended by germ cells.

RESULTS

The results of the six samples in the months April–September are displayed in the smoothed frequency polygons in Fig. 2. The weights of the leeches were recorded in 10 mg. classes, but instead of plotting the raw data as frequency polygons, the outlines were smoothed by taking a moving average of three points, i.e. each point represents the mean of its own class, the one above, and the one below. It was found that the major trends were displayed more effectively by this method. Leeches which showed a clitellum were treated as a separate population, and their frequency polygon drawn separately. The filling of the vasa deferentia with germ cells was found to coincide with the appearance of the clitellum.

In the May sample three distinct populations can be recognized: *A*, small leeches with no clitellum; *B*, larger leeches (100–300 mg.) showing the clitellum; and *C*, very large leeches (over 370 mg.) also showing a clitellum. Each of these populations is bimodal, and there seemed to be three possible interpretations of this fact: that each population is a single year-group but there are two races within the species; that each population is a single year-group but the eggs of the previous year had been laid in two broods; or that each population is composed of more than one year-group.

The first of these suggestions is given added weight by the fact that Johansson (1910) divided the species into three varieties, two of which are represented in this population. These are *E. octoculata* var. *atomaria* which has the dorsal surface marked by a black reticulum, and *E. octoculata* var. *vulgaris* which has a small amount of black pigment, not forming a complete reticulum, on the dorsal surface. It was thought possible that the two varieties might differ in their mean weights, thus accounting for the bimodality. To test this, the May sample was separated into the two varieties, and the frequency-distribution of weights recorded in Table 1. The value of χ^2 is 7·70 which is not significant at the 5% level of probability, so it is clear that there is no significant difference in weight between the two varieties.

The second possibility, that the young of a particular year are produced in two broods, was investigated by taking a census of cocoons as previously described. Fig. 3 shows the number present on successive dates and, in addition, a line has been drawn to show the rate of cocoon production, calculated by taking the mean of successive five-day periods. The curves show that the cocoons were not laid in a single batch, but that there were peaks of production in mid-June and mid-July. This explains satisfactorily the bimodality of the populations. The June-born leeches will appear as a heavier component and the July-born leeches as a lighter component in any year group.

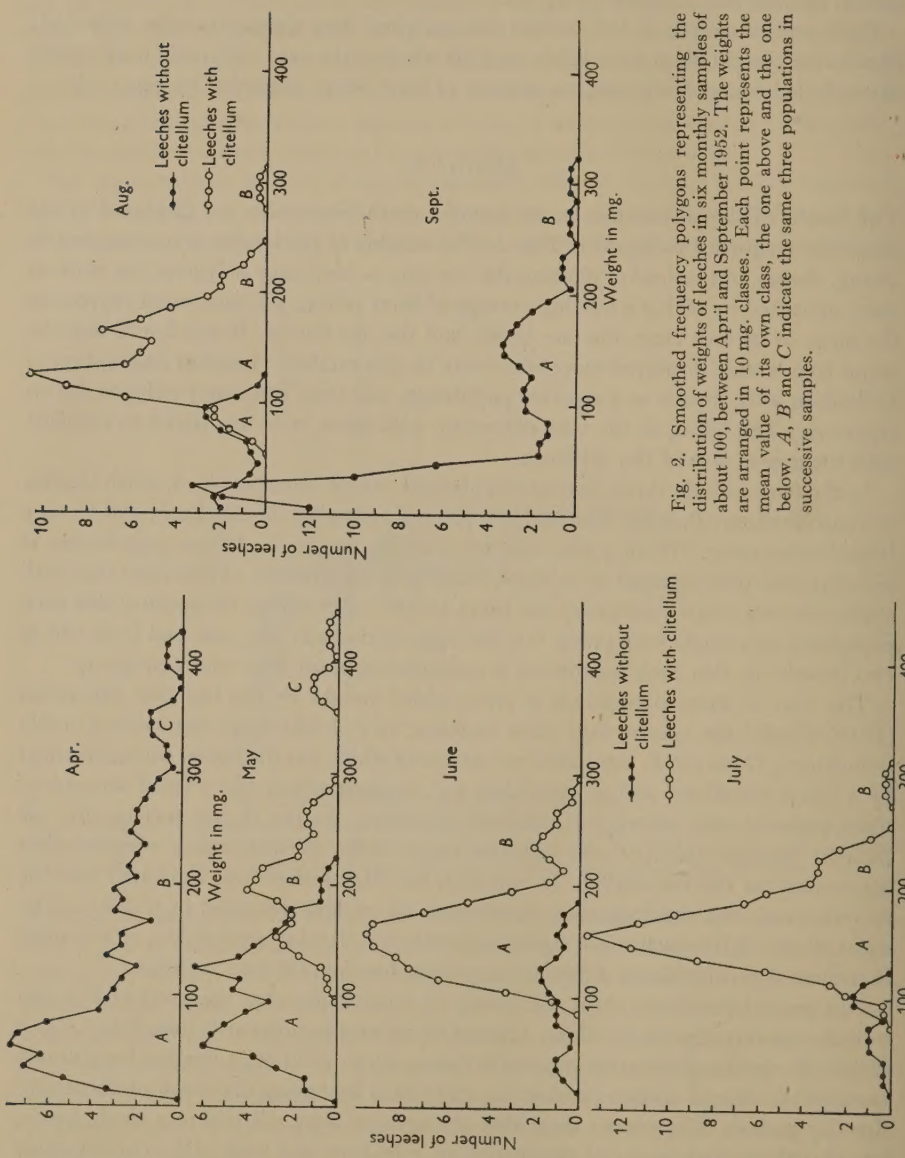

Fig. 2. Smoothed frequency polygons representing the distribution of weights of leeches in six monthly samples of about 100, between April and September 1952. The weights are arranged in 10 mg. classes. Each point represents the mean value of its own class, the one above and the one below. *A*, *B* and *C* indicate the same three populations in successive samples.

The third explanation of the bimodality now appears unlikely, and may be dismissed after following the fate of each population through the series of samples. In June nearly all the leeches had a clitellum. Leeches between 0 and 200 mg. are thought to belong to population *A*, population *B* is represented by a small number of leeches between 200 and 300 mg., and population *C* is not represented.

The first set of cocoons, which we have seen were deposited in mid-June, must have been produced by populations *B* and *C*, and since most of population *A* had developed clitella by the end of June, while *B* and *C* had almost disappeared we may suppose that *A* was responsible for the July brood.

Table 1. *Frequency distribution of weights of the two varieties of* Erpobdella octoculata

	Weight (mg.)						
Variety	40–79	80–119	120–159	160–199	200–239	240+	Totals
vulgaris	9	8	6	2	6	3	34
atomaria	14	10	16	17	6	6	69
Totals	23	18	22	19	12	9	103

$\chi^2 = 7{\cdot}70$.

The July sample of leeches consists almost entirely of population *A*, with population *B* represented in the 'tail' at 200–300 mg. In August the picture is similar, except that a few specimens of less than 40 mg. are present, and these are obviously newly hatched.

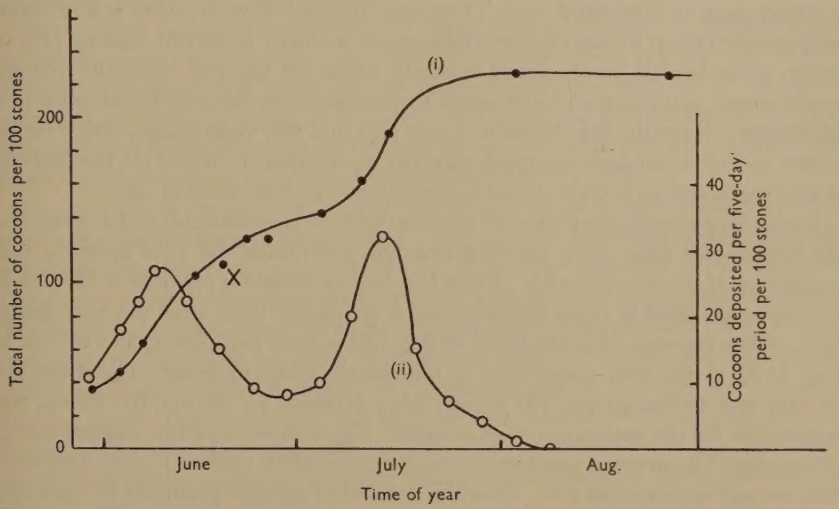

Fig. 3. (i) The total number of cocoons present on 100 stones, at short intervals of 4–7 days. (ii) The number of cocoons deposited on 100 stones in each successive 5-day period, calculated from curve (i). At *X* the substratum was disturbed by cows.

In September the newly hatched leeches form two-thirds of the sample. The remainder are mainly population *A*, with just a few of population *B*. Returning to the April sample, it is clear that the same three groups are present as in September, and

comparing this with May it is possible to identify population *A* as the leeches hatched the previous summer. By following the cycle through again, it may be shown that population *B* in May is composed of leeches about 20 months old. After breeding at 23 months of age, all but a small number of these disappear from the samples. Observations in the laboratory have confirmed that most of this age-group die soon after breeding, and in the stream it took much longer to collect 100 in July than it did in May.

Many of the leeches between 70 and 110 mg. in the August sample were specimens which failed to reach maturity in their first year of life. It seems reasonable to suppose that these are the individuals which survived the breeding season at two years of age and lived to breed at the end of the third year of life—population *C*.

There is therefore no doubt that populations *A*, *B* and *C* in the May sample are three-year groups, 0+, 1+ and 2+ years of age.

DISCUSSION

It is now possible to outline the life history of a year-group. The cocoons are laid by the parents in June or July, and the young leave the shelter of the cocoons in August and September. In the July of the following year most of these leeches come to maturity and breed, but rather less than 13% of them, the smaller individuals, fail to do so. In the second year of life all the year-group comes to maturity and breeds during June. Subsequently all but the odd 13% die. Presumably those which survive are the individuals which failed to reach maturity in their first year of life. These live to breed again in their third year. Three conclusions follow: (i) there is a minimum body weight (about 60 mg.) below which sexual maturity cannot be attained; (ii) the larger, older leeches reach sexual maturity earlier in the year than the younger, smaller ones; and (iii) each leech seems to possess the capacity to breed twice in its life history. Normally this happens at one year and two years of age, but if for any reason an individual does not reach maturity at one year, it breeds for the first time at two years, and lives on to breed a second time at three years of age.

In the May sample there were 67 one-year-old, 34 two-year-old, and 4 three-year-old leeches. All these were potential breeding individuals for 1952 except a small proportion of the one-year-olds. From the August sample it seems that 13% of the one-year-olds failed to reach maturity, and if we deduct these from the May sample, 13% of the one-year-olds are equal to 9% of the total population, and we are left with 91% of the May population as individuals about to breed. The density on 30 May was 49 leeches per 100 stones; 91% of these, i.e. 45 per 100 stones, were responsible for the season's crop of cocoons. Fig. 3 shows that this totalled 225 per 100 stones. The average number of young contained in each of a large number of cocoons was estimated as 4·70. Thus the number of cocoons produced by each leech works out at 225/45, i.e. 5, and the number of young produced by each leech as $5 \times 4{\cdot}70 = 23{\cdot}5$.

For every leech breeding in 1952 an average of 23·5 young were produced. If the population remains at the same density each year, only one of these leeches will live to breed at two years of age, so that the gross mortality is 22·5/23·5 in two years, but we wish to know whether there is a steady mortality throughout life, or whether some

stage in the life history is critical. One fact which stands out is that in the samples the ratio of one-year-olds to two-year-olds was approximately 2:1. In May 1952 the figure was 67 : 34 and in September when the young were not all hatched, the ratio of newly hatched to one-year-olds was 64 : 37. Similar ratios were obtained in some trial samples taken in 1951, so it looks as if it is a characteristic of the population as a whole. We may thus infer that 67 leeches in 1951 are reduced to 34 by the same month in 1952, so that the mortality rate is roughly 50% per annum for that part of the life history which is reflected in the sampling. If we assume that the newly hatched leeches have all emerged from the cocoons in October, we are able to follow them through the whole of the next year, and on to the breeding period in the subsequent year, about 20 months in all. A mortality of 50% per annum may be represented by the equation $P' = P/2^x$ where P is the number of leeches originally present, and P' is the number present after x years. Using this, we may calculate that 1 two-year-old leech breeding in June is represented by 3·17 newly hatched leeches 20 months previously. The difference between the 23·5 leeches produced by a single parent and the 3·17 present in October must be accounted for by supposing that a mortality of about 86% occurs in the first three to four months of life. That this does in fact occur may be confirmed by tackling the problem in another way. In May 1952 there were 49 leeches on 100 stones, and 67/105 of them were 10 months old, so the actual number of this age-group present on 100 stones was $67/105 \times 49 = 31$. We have calculated that at this stage of the leeches' life history the mortality-rate is about 50% per annum, so we may estimate that the number of leeches aged 15 months in October is only 24·6 per 100 stones.

Now if there had been no mortality of newly hatched leeches, the number present on 100 stones in October would have been $23{\cdot}5 \times 45 = 1057{\cdot}5$, and the ratio of newly hatched to 15-month-old leeches in the sample would have been 43 : 1. In October collecting was difficult owing to a rise in water-level, but a small sample of 42 was obtained, and the ratio of newly hatched to one-year-olds was 3·9 : 1. This figure could only be obtained if there had been a mortality of 90·7%.

Clearly then, of the 23·5 young produced on an average by each leech, about 20 are lost during the first three or four months of life, and the remainder have their numbers halved during each subsequent year of life. It has been recorded by Bennike (1943) that a large number of cocoons are opened by molluscs, and their contents devoured. The most numerous mollusc in Foudry Brook is *Ancylastrum fluviatile* (Müll.). Larger specimens of *Erpobdella* are eaten by birds, for there are several helminth parasites which pass part of their life history in a duck and part in *E. octoculata*. The author has also noticed that in captivity the larger leeches tend to eat the smaller ones. It is probable that the heavy mortality in early life is attributable to molluscs and to cannibalism, while the lighter mortality among larger leeches is due to the predations of birds, and possibly also fish.

In the May and September samples, but not in the others, the three age-groups may be separated with confidence, and their mean weights calculated. The results have been plotted on a semilogarithmic scale in Fig. 4. The four round dots are the mean weights of the whole year-groups starting with the newly hatched leeches, and ending with the two-year-olds about to breed. The triangular dots are the mean

weights of populations consisting entirely of leeches which do not breed in the first year of life, but live on to three years of age. (The figure for 13 months was obtained from the August sample.) The curve connecting up the round dots suggests the growth curve for the population as a whole, and the curve connecting the triangular dots suggests the growth curve for those living the extra year. We see that the latter are leeches which grew slowly in the first year of life, and we may suppose that either these individuals were the last of the season's batch of cocoons to hatch, or for some reason they failed to obtain an adequate supply of food. Whatever the cause of the slow rate of growth, these leeches were below the mean weight of the population,

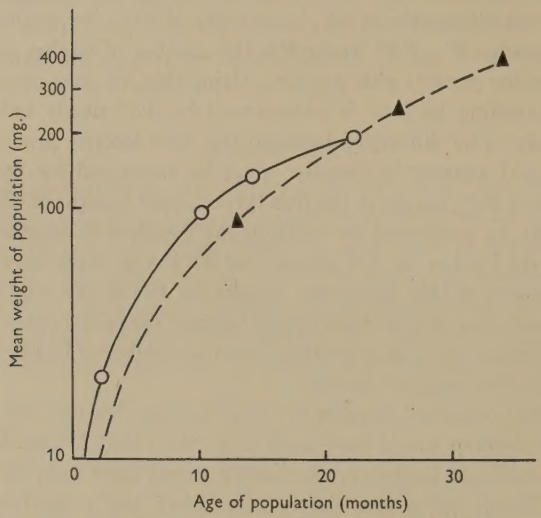

Fig. 4. The curve of $\log n+1$, where n=mean weight of population in mg., plotted against age of population in months.

and failed to reach sexual maturity in the first year of life. They would therefore continue to feed and grow during the time when their contemporaries were breeding and, by the age of two years, were of the same mean weight as those which had produced cocoons at one year. Breeding at two years of age occurred in both sections of the population, but those which were breeding for the first time lived on for a third year, growing steadily until their weight was nearly double what it had been at two years of age. They then produced their second batch of cocoons, and died.

ACKNOWLEDGEMENTS

I wish to thank Prof. A. Graham for reading and criticizing the manuscript, Mr M. I. Crichton for practical assistance on several occasions, and Mr G. Williams for his valuable advice at all stages of the work.

SUMMARY

1. The life history of *Erpobdella octoculata* (L.) was investigated by taking samples of about 100 at intervals of one month, and weighing each leech separately. A simple spring balance was devised for the purpose.

2. The life history was found to be as follows. Cocoons are laid in June and July, and the young emerge during August and September. By the following summer most of these are mature and deposit cocoons in July, but about 13% fail to reach maturity that year. In the next year the whole age-group becomes mature, deposits cocoons in June, and dies, with the exception of the leeches which did not breed in the first year of life. These breed in the second year of life, but live on to breed for the last time at three years of age.

3. Because the 0+ year-group breeds in July and the 1+ year-group in June, the cocoons are deposited in two batches, and the year-group is bimodal. There is no evidence that the species is divisible into two races on the basis of breeding habits or weight.

4. Each leech produces, on the average, 23·5 young per year, of which about 21 are killed during the first four months of life. Subsequently, their numbers are halved in each year of life.

5. The leeches which do not breed in the first year, but live on for three years, are those which grow more slowly at first, catch up with their contemporaries in the second year, and then grow on steadily for a third so that their final weight may be double that of a normal two-year-old.

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THE ECOLOGY OF ROTIFERS IN CAMBRIDGESHIRE

By ERNEST A. GRAY

24 Chesterton Hall Crescent, Cambridge

(With 1 Figure in the Text)

This paper summarizes observations made on Cambridgeshire rotifers during the past six years, on the one hand in random samplings of a variety of habitats throughout the county in a search for rotifers, and on the other hand during some particular investigations of the River Cam and a swift chalk stream (Hobson's Brook) which had the primary object of studying the association between their bacteria and ciliate protozoa (Gray 1951*a*, 1952).

METHODS

Samples were taken in sterile 8 oz. bottles or in chemically clean but not sterile small glass bottles with a capacity of 80 ml. and a rubber stopper. Samples were always examined within three hours and often within an hour of being taken. A small quantity was withdrawn by pipette and examined by direct and dark-ground illumination. In the studies of the Cam and Hobson's Brook, after the requisite amount had been withdrawn and the pH ascertained, the remainder was centrifuged, or filtered through sand and gauze following the method described by Whipple (1914). This was found to be time-consuming, so it was given up in favour of estimations of abundance only (cf. Hausman 1917). No accurate estimations of abundance were made of the rotifers. Random samples were seldom filtered or centrifuged. Specimens could often be obtained more easily if the water coating the vegetable material was allowed to drip on a slide, or the vegetable matter was agitated in a dish and the contents allowed to settle in a conical funnel. The former method proved more effective.

The investigation on the River Cam was carried out from May to November 1945, samples being taken from approximately 2 in. beneath the surface (plankton) and from the bottom at a depth of 4 ft. (benthos). Hobson's Brook was examined from October 1946 to October 1948 and a few additional weeks, while the random samples were collected during the past six years, chiefly from May to September.

HABITATS EXAMINED

The samples came from habitats which may be classified by their turbulence. Hobson's Brook has a linear rate of flow varying between 2 and 0·2 ft./sec. The River Cam and the River Rhee at Shelford have an average rate of flow about 0·2 ft./sec. Further samples were taken from the River Cam at Byron's Pool, where the water falls over a weir, and from the Bourn Brook, which has a very sluggish and at times negligible current. All these streams are alkaline in reaction, with an average pH in the region of 7·5. The current in the Bourn Brook is so slow as to approach the dykes from which other samples were taken. Many of these ditches are of considerable age, and are

usually stagnant except after rain. The least turbulent waters of all were those of ornamental lakes at Madingley Hall and Audley End House and various ponds sampled. The pH of the water in the dykes and still water varied between neutral and 7·5 according to the district and the nature of the vegetation.

GENERA IDENTIFIED

Representatives of most of the families of the great Sub-Orders were found. All were free-swimming, no sessile forms being met with at any time. In view of my former experience therefore (Gray 1943) I wonder whether the latter are more rare to-day than the old works (e.g. of Pritchard 1852) would indicate was formerly the case. The following list, based on the classification of Wesenberg-Lund quoted by Jennings (1934) gives the names of species identified. Identifications are based not only on this author but also on Pritchard (1852) and the classic monograph by Hudson & Gosse (1886).

NOTOMMATIDAE
Diglena forcipata?
Furcularia longiseta
Notommata aurita?
Proales werneckii

SYNCHAETIDAE
Synchaeta tremula

SALPINIDAE
Diaschyzia hoodii
Diplois propatula
Salpina mutiga

EUCHLANIDAE
Cathypna luna
Distyla inermis
Euchlanis macrura
E. triquetra
Monostyla lunaris?

RATTULIDAE
Rattulus cylindricus
R. latus

COLURIDAE
Metopidia ehrenbergii
Stephanops muticus

DINOCHARIDAE
Dinocharis pocillum
Scaridium longicaudum

HYDATINIDAE
Hydatina senta

NOTOPSIDAE
Notops brachionus

ANURIDAEA
Anuraea sp.
A. cochlearis?

BRACHIONIDAE
Brachionus pala
Noteus quadricornis

PTERODINIDAE
Pterodina patina

PHILODINIDAE
Rotifer vulgaris
R. neptunis?
Philodina sp.
Callidina sp.

ECOLOGY

During the particular investigations on the River Cam and Hobson's Brook, the cycles of all other organisms were recorded, including those of the rotifers. Not only were temperature and pH noted, but changes on the land through which the streams flow, since the fertility of the water is influenced by agricultural operations on land draining into the water. Evidence accrued that the ciliates of soil and inland waters are largely identical (Gray 1948), and it is of interest therefore that a very attenuated species of *Rotifer* (*R. neptunis*?) first found in the soil near Hobson's Brook was later encountered swimming in the River Cam at Bryon's Pool. It is well known, of course, that certain Bdelloids can resist desiccation, and *R. vulgaris* and *Philodina* were found not only in the brook but in the soil of adjacent fields.

(*a*) *Temperatures*

Rotifers were encountered all the year round in Hobson's Brook, which had the lowest average but the most uniform temperature of all the habitats, being constant about 10–12° C. Only the same species were met with each year. In the River Cam, where a temperature stratification was noted, a variety of rotifers were encountered, at temperatures ranging from 9 to 20° C. The only rotifers common to the River

Table 1. *The seasonal appearance of illoricate and loricate rotifers, showing the tendency of the latter to appear during the summer months only*

Species	Habitat	Month	Temperature (° C.)
	ILLORICATE		
Callidina	Bourn Brook	Jan.	—
	R. Cam	Nov.	11
	Madingley Lake	June	—
Hydatina	Hobson's Brook	Feb.–Mar.	10
		Dec.	11
Philodina	Hobson's Brook	Jan.	8
Rotifer vulgaris	R. Cam	June–Nov.	13·5–19
	Hobson's Brook	Jan.–June	9–11
	LORICATE		
Diglena	R. Cam	July	18
	R. Rhee	Aug.	16
Dinocharis	Bourn Brook	Aug.	—
	R. Cam	Oct.	13·5
	Hobson's Brook	Aug.	12
Diaschyzia	Hobson's Brook	June	12
	Latham Rd.	Aug.	—
	Madingley	June	—
	R. Rhee	Aug.	16
Euchlanis	R. Cam	June–Aug.	14–19
	Hobson's Brook	Jan.–July	9–12
	Latham Rd.	Aug.	—
	Wicken Fen brick pits	Aug.	—
Furcularidae	R. Cam	June–Aug.	14–19
	Hobson's Brook	July	12
Monostyla	R. Cam	July	19
	Madingley Lake	June	—
	R. Rhee	Aug.	16
Notops	R. Cam	July–Aug.	18–19
	Clayhythe	July	—
	Latham Rd.	—	—
Pterodina	Burwell	June–July	—
	R. Cam	Sept.	16
	Clayhythe	June	—
	Wicken Fen brick pits	Aug.	—
Rattulus	Burwell	June–July	—
	R. Cam	Aug.	19
	Latham Rd.	Aug.	-
Salpina	Audley End	Aug.	—
	Latham Rd.	Sept.	—
	Madingley Lake	June	—
	Trumpington Rd.	Aug.	—
Scaridium	Bourn Brook	Sept.	—
	Latham Rd.	Aug.–Sept.	—
	Wicken Fen brick pits	Aug.	—

Cam and Hobson's Brook were those which can tolerate a wide range of temperature variations, e.g. *Rotifer vulgaris* 9–19° C., *Euchlanis* 14–20° C., or which appeared in the River Cam at low temperatures approaching the summer temperatures of the brook, e.g. *Dinocharis pocillum* at 13·5° C. and *Stephanops* at 16° C. *Stephanops* was also prominent in the River Rhee in August at temperatures about 16° C.

There was a broad seasonal cycle in Hobson's Brook, in that illoricate forms, notably *Hydatina senta*, were most common in the spring, whereas loricate forms such as *Dinocharis pocillum* appeared in the summer. The majority of the loricate species found in the River Cam appeared in summer as did those of the random samples from other habitats. At Burwell Fen, for example, Anuridae were encountered in the spring, but later in the year they were replaced by swarms of Rattulidae. Brachionidae were very common in August in dykes near Canteloup Farm and in the Bourn Brook, and during the same month *Scaridium*, *Rattulus*, and *Diaschyzia* were abundant in ditches behind Latham Road, Cambridge. *Pterodina* and *Scaridium* were present in numbers during August in the brick pits at Wicken Fen. Table 1 shows this seasonal trend.

(*b*) *Oxygen-saturation and pH*

In Hobson's Brook the oxygen content of the water is always very near saturation point, although it is highest in winter and tends to diminish as the year advances in proportion to the abundance of other life. It varies from 5 to 7 ml. O_2/ml. from January–March to 3–5 ml. from June–August. In the River Cam and the Bourn Brook no estimations of dissolved oxygen were made, but the content is probably much less owing to the quantity of suspended organic matter. The same is probably true in general of the other habitats sampled, modified by the stillness of the water, which permits sedimentation and luxuriant plant growth with production of oxygen during photosynthesis. The great majority of the rotifers recorded were found in

Table 2. *Relative abundance of rotifers in the Burwell dykes during 1951*

Species	Quantity	Month	pH of water
Anuridae	Fairly numerous	Mar.	7·3–7·4
Rattulidae	Very numerous	June	7·8–8·0
Rattulidae, *Pterodina*	Numerous	Aug.	8·0–8·2

alkaline waters. The River Rhee, the River Cam, the Bourn Brook and Hobson's Brook are all chalk streams, or receive surface water from chalk underlying the particular district of Cambridge. The same was true of rotifers from other habitats; they were most abundant in waters whose reaction was well above neutral point. In those few cases when the water had a pH between 6·5 and 6·0, only an occasional *Rotifer vulgaris* or *Philodina* was found. There was some suggestion that increasing alkalinity favoured multiplication, since in Hobson's Brook and the River Cam loricate species were most common during the summer months, when the pH rose steadily from about 7·2 to a maximum of 7·8 or 8·0. In the dykes at Burwell there was a distinct contrast in the rotifer fauna found in the spring (pH 7·3) as compared with that of August, when the pH was in the region of 8·1 (Table 2).

(*c*) *The influence of other organisms*

The flowering plants (Phanerophyta) found in the habitats were typically those characteristic of alkaline waters, e.g. *Nasturtium officinale* R.Br., *Apium nodiflorum* L. (Lag.), *Veronica anagallis aquatica* L. Their abundance did not appear to affect the numbers of rotifers except at the end of the summer, when as they began to die the pH of the water fell to the acid side while the water itself grew foul. This was very noticeable on more than one occasion in the dykes sampled, where large numbers of Brachionidae, for example, disappeared within a week as a growth of *Nasturtium* decayed, until only an occasional bdelloid could be found. There was an excessive growth of *Nasturtium* in Hobson's Brook in August 1948, attributable to a conjunction of heavy manuring of the land with a spell of hot weather, which completely choked the stream and converted it into a stagnant swamp from which rotifers completely disappeared. In Hobson's Brook, too, there was a seasonal peak of dipterous larvae

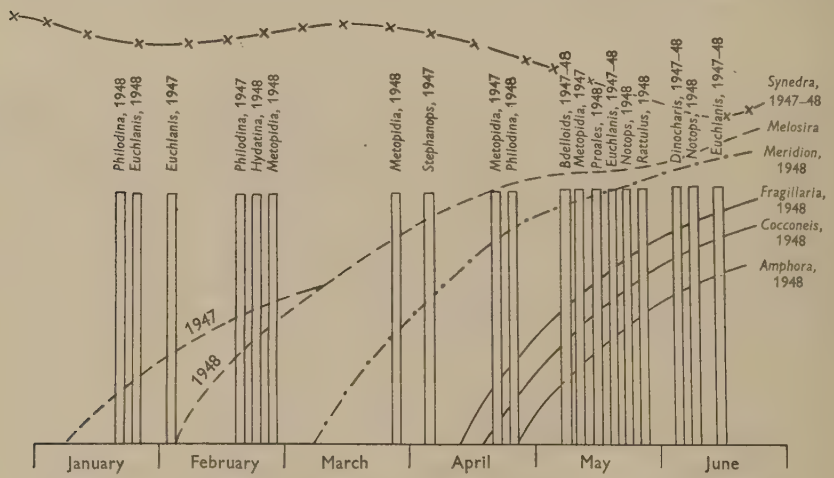

Fig. 1. The association between maximum abundance of diatom species and rotifers in Hobson's Brook during the two years 1947 and 1948.

each summer which depressed not only the numbers of protozoa but also the numbers and variety of species of rotifers. Diatoms were very common in all the habitats sampled, but most of all in Hobson's Brook where they were abundant all the year round. There was a peak of multiplication of diatoms in all the waters sampled in the spring and autumn. In Hobson's Brook, the numbers of rotifers and the numbers and variety of species of diatoms tended to increase together in the early months of the year (Fig. 1). This was a general finding at all seasons in other localities, that is to say, when certain diatoms were dominant in a particular water, certain rotifers appeared within a few days. *Rattulus*, for example, was abundant at Burwell, at Clayhythe, in the River Cam and Hobson's Brook, when *Synedra* and *Fragilaria* were dominant. *Dinocharis* was abundant in Hobson's Brook and the River Cam when *Synedra* and *Gomphonema* were dominant, and *Notops* in the same two streams when *Fragilaria* was most numerous. Table 3 exhibits this trend by showing how often nine species

of rotifers were found associated with four species of diatom and the green filamentous alga *Ulothrix*.

Analysis of the data by Mr D. V. Lindsey, of the University of Cambridge Statistical Laboratory, did not reveal any statistical significance in this table, in part because the numbers are too small to permit any definite conclusions. The only result which approached significance was the association of *Fragilaria* with *Euchlanis* as compared to that of other rotifers.

Table 3. *The association of certain rotifers with some members of the phytoplankton*

	No. of times observed	*Fragilaria*	*Meridion*	*Synedra*	*Gomphonema*	*Ulothrix*
Euchlanis	18	14	9	13	7	16
Notommatid	1	1	1	0	0	0
Bdelloid	5	1	2	4	0	2
Stephanops	8	3	2	6	5	4
Notops	7	3	1	5	2	6
Rattulus	4	2	3	4	2	3
Dinocharis	5	3	2	3	1	3
Pterodina	3	1	1	3	2	1
Metopidia	14	4	2	11	11	5

In Hobson's Brook and the River Cam no single rotifer or group of rotifers was found to be associated with any particular species of bacterium or of bacterial numbers at 22 or 37° C. In the two streams concerned *Euchlanis*, for example, was associated with a range of numbers from 2000 to 97,000 per ml. at 22° C. and up to 116,000 per ml. at 37° C., and *Stephanops* and *Rotifer vulgaris* with a range from 3000 to 400,000 and 36,000 to 96,000 per ml. at 22° C., and 21,000 and 16,000 per ml. at 37° C. The range of bacterial numbers found associated with certain rotifers is given in Table 4.

DISCUSSION

All the rotifers found favoured alkaline water. This agrees with my former experience (Gray 1935, 1943) that pools and streams on boulder clay with a neutral or alkaline reaction supported the greatest variety of infusorial life. There would appear to be grounds for a division into warm-water forms, and cold-water forms possessing, however, a wide range of temperature tolerance. Table 1 shows that the majority of loricate species are presumably warm-water forms in that they appeared in the summer months. Yet although the water of Hobson's Brook, which has the lowest average annual temperature, is nearly always saturated with oxygen, there was no profusion of cold-water forms. On the other hand rotifers were abundant in the depths of the River Cam or the Bourn Brook and in the dykes, where the oxygen content must have been considerably less owing to the quantity of suspended organic matter. Allen (1926) observes that 'there is not much profit in looking for a single determining factor in problems of natural environment', and in considering these physical factors of chemical reaction, temperature and oxygen content of the water it is plainly evident they are too closely interwoven for one to be considered without the

other. Food supply is probably the most dynamic factor in the ecology of rotifers. Table 3 suggests that food largely consists of diatoms, and possibly, to a lesser degree, of soft-bodied, or filamentous, algae. The figures given are not statistically significant owing to the smallness of numbers of samples, but they may provide a useful suggestion. It is common to see stomachs of rotifers stuffed to bursting with diatoms, and certain species (e.g. *Notops*) extrude their jaws to gnaw them off the surface of plants. On occasion rotifers may also be seen browsing on green algae, or the latter may be

Table 4. *The range of total bacterial numbers, and of bacteria classified on morphological grounds, found associated with rotifers in the River Cam and Hobson's Brook*

Species	Bacterial counts, thousands per ml. 22° C.	37° C.	Character of bacteria
		River Cam	
Anurea	8–9·3	4·5	Not known
Brachionus	5·5	—	
Dinocharis	8·2–16	4·8–96	
Euchlanis	3·2–32	1·4–34	
Furcularids	2·5–8	0·8–4·5	
Notops	0·3–28	2·2–45	
Noteus	3·4–4·5	7·6–8·0	
Rattulidae	2·8	32	
R. vulgaris	0·3–96	1·6–45	
Stephanops	21	56	
		Hobson's Brook	
Euchlanis	2–97	—	Micrococci Gram-negative and Gram-positive bacterial rods
Metopidia	5–56	Not known	Micrococci alone, micrococci and Gram-negative bacterial rods, micrococci and Gram-negative and Gram-positive bacterial rods
Stephanops	3–400	Not known	Micrococci alone, Gram-negative rods alone, micrococci and Gram-negative and Gram-positive rods
Diplois	12–87	Not known	Mixtures of Gram-positive and Gram-negative bacterial rods and micrococci
Philodina	32–36	Not known	Micrococci alone, mixtures of Gram-negative and Gram-positive rods
R. vulgaris	21–54	Not known	Mixtures of micrococci and Gram-negative and Gram-positive rods

seen in their stomachs, though far less commonly than diatoms. *Ulothrix* was found frequently associated with *Euchlanis* (Table 3). As regards the Blue-green algae, Edmondson (1947) states that 'some of the most rapid increases in Euchlanid rotifers coincided with a bloom of *Oscillatoria*, and some of the apparent effects of temperature may be attributed to a fair correlation between the concentration of *Oscillatoria* and temperature: *Euchlanis* did not appear in numbers till the temperature passed 15° C.' This was not in accordance with my findings. *Euchlanis* appeared *after* blooms of *Oscillatoria* in Hobson's Brook, and on two occasions two or three days after a bloom of *Anabaena* in the River Cam when the temperature of the water was 20° C. In the

absence of exact figures, the conjunction of an increase of diatoms and of rotifers, shown in Fig. 1, can only be shown as a general association, which does not as it stands prove a food relationship. If it is accepted as such, however, it is of interest that the hypotrichid ciliate *Stylonichia mytilus* undergoes cycles of abundance related to a lunar periodicity of diatoms on which it feeds (Gray 1951*b*, 1952). Such a periodicity might materially affect the abundance of other organisms (e.g. rotifers) which also feed on diatoms. Newmann (quoted by Welch 1935) distinguishes a group of rotifer species in which discrimination occurs in larger particulate foods and in which a predatory habit exists, from another one, probably the larger, in which food discrimination is slight or absent, the particulate substances in the water being taken as they come. Even if allowance is made for the smallness of the numbers, Table 3 points to some discrimination by rotifers for certain species of diatoms. Bacteria may be regarded as 'particulate substances' in the water, and from the range of bacterial numbers and species shown in Table 4 rotifers appear to have accepted them as they came. The figures are evidence that rotifers can tolerate very high bacterial numbers in water. Nevertheless, although there are species which can tolerate the putrescent liquids oozing from manure heaps, the great majority undoubtedly prefer clear water even if it has a high bacterial content. And numerous as the bacteria may be, there do appear to be concentrations lethal to rotifers. When water-cress choked Hobson's Brook and the bacterial count of the stream rose to close upon 10^6/ml. all rotifers disappeared. *R. vulgaris* has proved to be most sensitive to minute doses of the exotoxin of the tetanus bacillus which is common in soil and excreta (Gray 1941, 1943).

My experience further emphasizes the cosmopolitanism of rotifers to which Jennings (1934) refers. Any given species of rotifer could be found in Cambridgeshire, or for that matter in England, its presence depending not on the locality but on the conditions existing there. The physical factors temperature and pH appear to be more important than oxygen saturation, although the latter cannot be ignored. Rotifers favour alkaline waters, and some species, which it is suggested are warm water forms, are less adaptable to temperature variations than others. Whipple (1914) remarks that rotifers can be found at all seasons of the year but that they are most numerous in June and November. Food, as represented by algae, especially diatoms, would appear to be of supreme importance. Warm water species of rotifers may tolerate colder temperatures if attracted by abundance of their favourite food, but no form will be numerous if food is absent, however favourable the physical conditions. Temperature, food supply, and competition are stated to be the chief factors that influence seasonal distribution of Crustacea (Whipple 1914), and the same is also largely true of rotifers. Indeed, the very physical conditions that favour rotifers may also foster growth of their chosen foods, notably algae. Clear water, allowing free penetration of the sun's rays, is essential for growth of phytoplankton and this may be the reason why rotifers typically haunt such situations. For thereby they benefit not only by the solid foods provided by the plant cells, but also by the oxygen they give off, risking the bacterial numbers of the water, which are high in the vicinity of phytoplankton (Harvey 1945).

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SUMMARY

During the past six years, 30 species of rotifer have been identified in Cambridgeshire. They were all free-swimming forms; no sessile species were observed. They were found in a.variety of waters varying from a swift chalk stream to marshy pools in fen sedge but an alkaline habitat was always preferred. Whilst a preference was shown for warm waters, a temperature tolerance was exhibited by most. Food supply, as represented by diatoms particularly, is probably the dominant factor in their ecology. Loricate forms appeared to be most abundant during the summer months; but the nature of the species found in any water at a given season is determined by the conditions there existing, especially perhaps the pH and the existing food supply.

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THE MORTALITY, FECUNDITY AND INTRINSIC RATE OF NATURAL INCREASE OF THE MULTIMAMMATE MOUSE, *RATTUS* (*MASTOMYS*) *NATALENSIS* (SMITH)* IN THE LABORATORY

By W. D. OLIFF

Plague Research Laboratory, Department of Health, Johannesburg

(With 2 Figures in the Text)

For approximately four years (October 1946 to December 1949), records were collected on the length of life and the fecundity of female *Rattus natalensis* Smith in the laboratory. These records were tabulated and analysed in order to estimate the intrinsic rate of natural increase of the animals, together with their birth- and death-rates. The population parameters obtained refer to a laboratory population, and the results cannot be applied to field populations until field investigations confirm the findings.

METHODS

The mice were bred under fairly uniform conditions, for use as biological test animals for *Pasteurella pestis* organisms. The records were tabulated on individual breeding record cards indicating the origin of the animals, age at mating, dates of birth of litters and number of young born, together with number and sex of young weaned and, finally, age of the females at death or at the time of discarding. It is important at the outset to note certain limitations of the data. All females were mated with males of roughly similar ages before they were 112 days old, and in some cases were mated with litter-mates. In the event of a male dying or escaping and being lost to the experiment, another male of similar age was substituted. The females were thus, in effect, mated during the whole of their lifetimes. As they were, with few exceptions, mated to a particular male exclusively, there is a possibility that sterility or relative infertility of the male partner may have reduced the fertility figure of the female concerned. No males have ever been proved to be sterile during the experiments to date, and we have assumed that variations in male fertility are unimportant.

A further point to note is that 55 of the 176 females were discarded from the laboratory stock before the natural end of their lives, in the interests of laboratory productivity. These animals would have lived longer, so the true age at death in these cases is thus not known. A correction has been made for this in computing the life-table.

One other point of importance is that the animals have been selected for breeding ability. Only litters from females with proved breeding ability were mated for the breeding stock. This may mean that the breeding ability of our laboratory animals

* Most commonly referred to as *Mastomys coucha* Smith.

may be higher than that of a normal population. Such selection has only been in progress for at most four generations, and probably has not had time to produce any great differences in breeding ability which might influence our estimates of the population parameters. Despite these limitations the results should be of some value as they give an indication of the expectation of life of the females and the productivity that can be expected of them in the laboratory.

The stock was derived from a number of wild mice captured in the vicinity of Johannesburg. The line has been bred for a number of years, and the animals providing the data in these records are between one and four generations removed from their captured ancestors. The mice were mated, placed in $12 \times 8 \times 4$ in. metal cages and housed in rooms kept at a temperature of $65 \pm 6°$ F. The illumination was normal daylight. The stock was fed on 'Comproid' biscuits daily and with carrots three times a week. Water was provided in drop bottles fixed in the roofs of the cages. Bedding material of sawdust and straw was provided which was replaced once a week. The animals were examined daily, except Sundays, and data were recorded daily.

LIFE-TABLE DATA

No useful records of the life histories of the males exist. The life-table was thus based exclusively on data collected for females. Males, however, usually outlived females (in 163 out of 176 cases) and the life-table may be taken as giving the minimum expectation of life of the males. Females died of two major causes. The first was pneumonic involvement of some sort, and the second, obstetrical obstruction or complications on parturition. We do not know if such causes of death obtain in the field. A rather coarse grouping into 28-day age-intervals has been employed. As the animals all entered the experiment as adults (i.e. over four weeks old), mortality figures for the nil to eight-week age-groups were derived from the mortality observed in the progeny of the experimental animals.

The life-table was constructed using the recognized method which allows for individuals lost or removed from the experiment. The distributions used were:

a_x = the number of accidental deaths, losses or removals during the interval x to $x+1$,

d_x = the number of true deaths in the interval,

n_x = the number of individuals known to be alive at the exact age x at the beginning of the interval,

b_x = the number entering during the interval;

from which the following distributions were computed:

$q_x = d_x / \{n_x + \frac{1}{2}(b_x - a_x)\}$,

$l_x = p_0, p_1, p_2, \ldots, p-1$,

$L_x = \frac{1}{2}(l_x + l_{x+1})$ (approximating to the integral).

The true life-table (L_x) is given in Table 1. The first age-group presented a little difficulty. An approximate value for L_0 was obtained as

$$\tfrac{3}{8}(1{\cdot}0000 + 0{\cdot}6637) + \tfrac{1}{8}(0{\cdot}6637 + 0{\cdot}6637).$$

This was derived from the mortality (0·3363), which was determined at the time of weaning, 21 days after the birth of the litters. Little mortality was found to occur

between the 4th and 8th weeks after birth so d_1 has been taken as zero. The l_x values have been used to construct a graph of the survival of the animals. This appears in Fig. 1. The curve is a complex curve with two major points of inflexion at about the 4th and 20th age-intervals. At present no useful comments can be made about it. One of the objects of our analysis was to obtain data on the age-specific fecundity rates of females under laboratory conditions. Table 2 gives these data.

The sex records of young at birth are incomplete, as the disturbance involved in handling caused a number of females to eat their litters and the practice was dis-

Table 1. *Life-table data for females*

x age interval (28-day units)	Nos. entering experiment	Nos. leaving experiment	No. of known deaths	l_x (beginning of interval)	True life-table, L_x
0	51	0	0	1·0	0·7898
1		0	0	0·6637	0·6637
2	95	1	1	0·6637	0·6603
3	30	3	3	0·6570	0·6508
4	—	4	4	0·6447	0·6372
5	—	9	8	0·6297	0·6146
6	—	16	15	0·5996	0·5712
7	—	7	7	0·5428	0·5295
8	—	10	9	0·5163	0·4991
9	—	8	8	0·4820	0·4667
10	—	9	8	0·4514	0·4360
11	—	6	4	0·4206	0·4128
12	—	8	7	0·4051	0·3912
13	—	8	6	0·3774	0·3653
14	—	6	4	0·3533	0·3451
15	—	4	3	0·3369	0·3306
16	—	5	2	0·3243	0·3200
17	—	2	1	0·3157	0·3135
18	—	3	2	0·3113	0·3068
19	—	6	2	0·3023	0·2977
20	—	3	0	0·2930	0·2930
21	—	6	5	0·2930	0·2803
22	—	13	6	0·2676	0·2510
23	—	10	7	0·2345	0·2126
24	—	10	3	0·1907	0·1795
25	—	3	1	0·1683	0·1636
26	—	6	3	0·1589	0·1425
27	—	5	1	0·1260	0·1182
28	—	4	0	0·1103	0·1103
29	—	1	1	0·1103	0·0551
30	—	0	0	0	0
Totals	176	176	121	—	11·4510

continued. The figures given for the sex of young born are derived from records of females which successfully reared all members of a litter. The sex ratio of the young at birth was found to be 0·51909 female (1889 males to 2039 females). On weaning the ratio was found to be lower, being 0·51001 female (2837 males to 2953 females).

The average productivity of females, obtained from the sums of the age-specific litter and birth-rates, is 0·45518 litter and 3·33309 young per female per 28 days. A female on the average thus produced 7·3223 young per litter, every 61·51 days. We have found it possible for a female to produce litters at approximately 26-day intervals, provided no oestrous cycles were 'missed'. In addition, it was found that

0·53 of the total female 'life-times' during the experiment were spent in anoestrus. This suggests that the stock animals produced litters only 0·47 times as frequently as was possible. Fairly lengthy periods may thus have occurred during which the females did not breed, possibly as a result of similar anoestrous periods. It is impossible to judge whether such non-breeding periods are a normal feature of the female breeding cycles in the field or whether they are induced by laboratory conditions and diet.

THE INTRINSIC RATE OF NATURAL INCREASE

The calculation of the intrinsic rate of natural increase was based on the method so lucidly described by Birch (1948), where the rate of increase of the population is given by $dN/dt = rN$ and the value of r is calculated from the expression

$$\int_0^\infty e^{-rx} l_x m_x dx = 1. \tag{1}$$

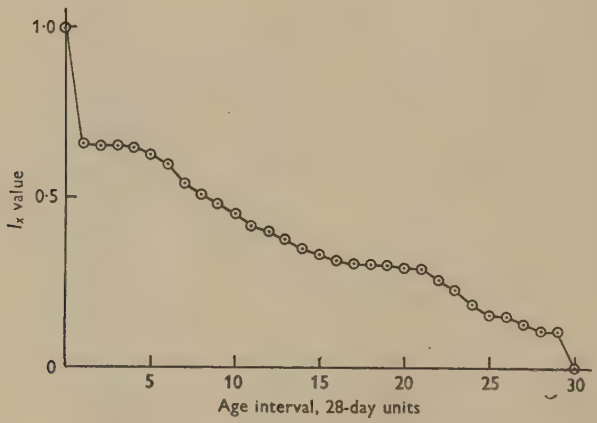

Fig. 1. The survival curve for *Mastomys* females.

The approximate method was used, for which we write

$$\sum_0^\infty e^{-rx} l_x m_x = 1; \tag{2}$$

x was taken as the mid-point of the respective groups. A number of trial values were substituted in equation (2) above. In each case a series of values for e^{-rx}, $e^{-rx} l_x m_x$, and $\Sigma\, e^{-rx} l_x m_x = 1$, was calculated. The value of r was thus found by trial and error which made

$$\Sigma e^{-rx} l_x m_x = 1.$$

The value found for r was 0·4068 (the true value probably lies between 0·40677 and 0·40678). This is the infinitesimal or intrinsic rate of natural increase. The finite rate of increase is antilog e^r. In this case the value is 1·502 per head per 28 days, i.e. the population will multiply 1·502 times per head per 28 days.

The value obtained for r (0·4068) was then used to calculate the stable age-distribution from the expression

$$\frac{1}{B} = \sum_{x=0}^{m} Lxe^{-r(x+1)},$$

where B = the number of births occurring in the stable population during the interval of one unit of time, divided by the total number in the population at the beginning of the interval. From this expression the stable age-distribution and the instantaneous birth-rate are obtained (see Table 3). The quantity $1/B$ has a value of 1·36741. B is,

Table 2. *Productivity of females*

Age-group in days	No. of females at risk	No. of litters born	Age-specific litter-rate	Total no. of young born	Age-specific birth-rate (males and females)	No. of litters weaned	No. of young weaned
–56	25·5	0	0	0	0	0	0
56–	98	8	0·0816	48	0·4898	4	20
84–	158·5	45	0·2839	338	2·1325	35	172
122–	170	84	0·4941	654	3·8471	71	440
140–	163·5	79	0·4832	648	3·9633	61	368
168–	151	73	0·4834	598	3·9603	56	346
196–	139·5	68	0·4875	578	4·1434	60	406
224–	131	84	0·6412	704	5·3740	70	467
252–	122	61	0·5000	495	4·0574	50	339
280–	113·5	63	0·5551	520	4·5815	58	408
308–	106	71	0·6698	575	5·4245	65	422
336–	99	60	0·6061	493	4·9798	53	333
364–	91	55	0·6044	452	4·9670	43	281
392–	84	46	0·5476	350	4·1667	39	204
420–	79	40	0·5063	304	3·8481	34	206
448–	74·5	43	0·5772	344	4·6174	34	226
476–	71	31	0·4366	225	3·1690	26	154
504–	68·5	37	0·5401	265	3·8686	30	175
532–	64	37	0·5781	263	4·1094	30	195
560–	59·5	31	0·5210	234	3·9328	28	185
588–	55	29	0·5273	190	3·4545	26	151
616–	45·5	26	0·5714	174	3·8242	18	105
644–	34	19	0·5588	112	3·2941	15	86
672–	24	16	0·6667	102	4·25	13	72
700–	17·5	10	0·5714	55	3·1429	7	33
728–	13	4	0·3077	19	1·4615	3	10
756–	7·5	3	0·4	12	1·6	2	5
784–	3	0	0	0	0	0	0
812–	0·5	0	0	0	0	0	0
Totals	176	1123	13·2005	8752	96·6598	931	5809

therefore, 0·73130. The fifth column of Table 3 gives the stable age distribution per total population of 100 individuals. It will be seen from the last column in the table, where the cumulative percentage of the stable age distribution is given, that over 50% of the stable population was less than 8 weeks old, 90% of the population was less than 20 weeks old. Of this 90%, approximately 16% only were adult animals (3 months old).

Using the above constants the instantaneous birth-rate of the population was computed from the relationship $b = rB/(e^r - 1)$. The birth-rate, b, is 0·59261 per head per 28 days and the death-rate is thus 0·1858 per head per 28 days, from the relationship $r = b - d$.

POSSIBLE SEASONAL VARIATION IN FECUNDITY

It will be of interest to apply these results directly to field populations as Leslie & Ranson (1940) have done for the vole but, as no field population statistics are available, we can do no more than suggest some possible conclusions which may or may not apply to the behaviour of such field populations. Laboratory observations suggest that there is a slight seasonal variation in the numbers of litters and young. This may mean that *Mastomys* has definite breeding and non-breeding seasons, or more likely that during certain periods of the year it breeds at a reduced rate. The periods may not be the same for all females and so there may be no true non-breeding season as

Table 3. *The stable age-distribution of the population*

Age-group (in 28-day intervals)	$e^{-r(x+1)}$	Life-table (L_x)	$L_x e^{-r(x+1)}$	Stable age-distribution	Cumulative percentage stable age-distribution
0	0·6658	0·7898	0·52584	38·455	38·455
1	0·4433	0·6637	0·29422	21·517	59·972
2	0·2951	0·6603	0·19485	14·250	74·222
3	0·1964	0·6508	0·12782	9·348	83·570
4	0·1308	0·6372	0·08335	6·095	89·665
5	0·0871	0·6146	0·05353	3·915	93·580
6	0·0580	0·5712	0·03313	2·423	96·003
7	0·0386	0·5295	0·02044	1·495	97·498
8	0·0257	0·4991	0·01283	0·938	98·436
9	0·0171	0·4667	0·00798	0·584	99·020
10	0·0114	0·4360	0·00497	0·363	—
11	0·0076	0·4128	0·00314	0·230	—
12	0·0050	0·3912	0·00196	0·143	—
13	0·0034	0·3653	0·00124	0·091	—
14	0·0021	0·3451	0·00072	0·053	—
15	0·0015	0·3306	0·00050	0·037	—
16	0·0010	0·3200	0·00032	0·023	—
17	0·0007	0·3135	0·00022	0·016	—
18	0·0004	0·3068	0·00012	0·009	—
19	0·0003	0·2977	0·00009	0·007	—
20	0·0002	0·2930	0·00006	0·004	—
21	0·0001	0·2803	0·00003	0·002	—
22	0·0001	0·2510	0·00003	0·002	—
23	0·0001	0·2126	0·00002	0·001	—
24	0	0·1795	0	0	—
25	0	0	0	0	—
Totals	—	—	1·36741	100·001%	—

such. Brambell & Davis (1941) have shown that in Sierra Leone some fecund male *Mastomys* are present at any season of the year. They found no evidence of a non-breeding season though there was a greater proportion of pregnant females in October and November than at other times. Their analysis of the distribution of body-weights throughout the year showed a high percentage of adult animals in August, September, October and November, and a high proportion of juveniles in February, March and April. They conclude that this indicates maximum breeding in August and September and a minimum from February to April.

The present study shows that immature animals will be 0–8 weeks old. Such animals would therefore have been born 0–2 months previously as the authors mention. Furthermore, we expect to find a high proportion of juveniles in an

increasing population, and a high proportion of adult animals in a decreasing, non-breeding population. Brambell & Davis suggest that a season of increased breeding occurs. The breeding season would commence 1–2 months before the proportion of juveniles in the catch begins to increase, in August–September, and would continue until February, i.e. there would be a winter-breeding season. If this is true the apparent coincidence of breeding with the late rains as reported by the authors is correct. The breeding season thus coincides with decreasing rainfall and the dry season. There thus seem to be some grounds for believing that in Sierra Leone breeding occurs in the winter and autumn months, though it is probable that reduced breeding activity occurs throughout the remaining months of the year. If this is the case in the equable climate of the tropics it is likely that a similar state of affairs exists in South Africa. For the present, for simplicity, we will assume that the whole population has a definite non-breeding season and an estimate of the rate increase of a population with varying lengths of breeding season will be made.

Table 4. *Rate of increase of a population with various lengths of breeding season*

Four-weekly periods of breeding season	Females surviving during non-breeding season P'_{52-t}	e^{rt}	$(P'_{52-t}e^{rt})$	r'_a
13	100·001	198·0	198·0	9·1901
12	92·449	131·8	121·85	7·6894
11	90·321	87·78	79·28	4·3730
10	87·370	58·43	51·05	3·9328
9	83·637	38·90	32·53	3·4822
8	79·021	25·90	20·47	3·0189
7	73·744	17·25	12·72	2·5432
6	68·994	11·48	7·92	2·0694
5	64·907	7·645	4·962	1·6018
4	60·988	5·090	3·104	1·1327
3	57·475	3·388	1·947	0·6663
2	54·443	2·256	1·228	0·2054
1	51·584	1·502	0·775	−0·2549
0	48·867	—	—	—

In order to arrive at some estimate of the rate of disappearance of the population during a non-breeding season, if such exists, a series of population tables was constructed to give the rate of disappearance of the Malthusian population in non-breeding seasons of various lengths. These values, at four-weekly intervals, appear in Table 4. If we assume that the reduced population will increase so as to approximate in time to the Malthusian form, then with the total numbers so obtained a value for the number of individuals at the end of a year can be estimated from the relationship $N = N_0 e^{rt} P'_{52-t}$, where P'_{52-t} is the probability of survival for the given time interval. The momentary rate of increase per annum is defined as $r'_a = \log (P'_{52-t}e^{rt})$. The respective values obtained for the relationship are given in Table 4.

The values of r'_a obtained for the respective lengths of the breeding season have been graphed (Fig. 2), and from the interpolated line we see that $r'_a = 0$ when $x = 44{\cdot}8$ days. That is, the population will maintain its numbers from year to year if breeding continues under the conditions of the experiment for approximately 45 days in the year. This indicates a tremendous breeding potential which can seldom even partially

be realized in nature, though plagues of *Mastomys* have been recorded but only on a few widely separated occasions.

DISCUSSION

In addition to the above parameters the age-specific litter-rates and the age-specific birth-rates have been calculated as these figures have an interesting application to populations in the field, a point suggested to me by Mr Leslie. The totals for these distributions give the approximate average litter-rate as 0·0709 per female per 28 days,

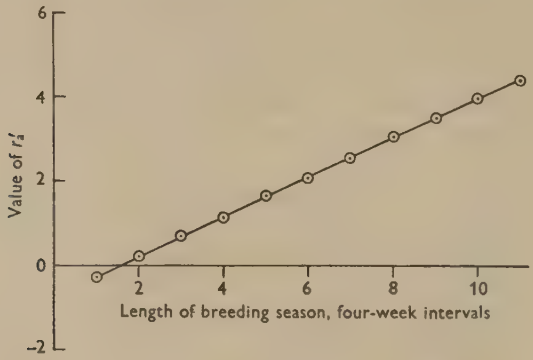

Fig. 2. The rate of increase of the population.

and the approximate average birth-rate as 0·5059 per female per 28 days, a value lower than that previously found by a more accurate method. Using the parameters found for the laboratory population an attempt can be made to find the composition of random monthly samples from a model field population with a six-month non-breeding season.

We have found that laboratory females mature at an approximate body weight of 39 g. There was considerable variation in the small sample in the ages at which the females attained this critical weight. The average age of the whole sample was 104 days on reaching maturity. An examination of the m_x distribution in Table 2 confirms that most of the females matured in the fourth age-group, as judged by their pro-

Table 5. *Percentage of juveniles in the population*

	Stable age, population	Length of non-breeding season			
		4 weeks	8 weeks	12 weeks	16 weeks
Juvenile	80·77	68·74	51·94	25·38	0
Adult	19·23	31·26	48·06	74·62	100

duction of litters. If we regard animals as mature at 104 days of age, 0·76428 of the stable population will be juveniles. As we can observe pregnancy in the animals for about three-quarters of the 23-day pregnancy period, we would expect to find 18·27 % of the females pregnant in a random sample of a field population which conforms to the Malthusian age distribution. The percentage of females which will be immature at various times during the non-breeding season is given in Table 5. Further we expect

the population to recruit itself in approximately 1½ months after a six-month non-breeding season. The theoretical model can now be constructed and appears in Table 6, together with the actual composition of the samples reported by Brambell & Davis (1941) for *Mastomys* collected in Sierra Leone. It should be noted that Brambell & Davis regarded 40 g. as the weight of the female when mature.

We have assumed that the theoretical population commenced to breed in November–December. In reality they started to breed in July–August, and continued breeding until April–May but, as will be seen from the figures, the increase was not large until November–December when the major increase commenced. The major breeding season then continued until about March when the population appeared to have a stable age-composition. After March the breeding apparently 'tailed off' gradually. The agreement between the model and the actual results is not good but is suggestive.

Table 6. *Age-composition of the* Mastomys *populations*

	Theoretical population (females)		Actual population (females)		Brambell & Davis (males and females)
Month	% Adult	% Pregnant	% Adult	% Pregnant	
January	85	→100	75	—	63
February	38	—	32	4	34
March	19	18	25	0	36
April	31	0	40	33	37
May	48	0	60	0	71
June	75	0	42	0	69
July	100	0	75	25	84
August	100	0	—	—	—
September	100	0	100	—	100
October	100	0	95	35	98
November	100	0+	100	100	93
December	100	→100	—	—	—

The natural population did not appear to increase at the same rate as the model and, in addition, the initial build-up was slow and the cessation of breeding gradual, as one might expect.

The percentage of females found pregnant in the field at different times of the year varied between 25 and 33%. This is higher than we might expect for a stable-age population. The samples are, however, extremely small, and it is possible that some selection in preference of the adults may have occurred in collecting the animals. The presence of pregnant females at different times throughout the year is evidence against strictly seasonal breeding. It shows, as the authors point out, that the animals do breed at all times, but nevertheless a definite season of increased breeding does occur roughly between the months of November and March. These results suggest that the rate of increase and rate of disappearance of the animals in the field in some ways resembles results established in the laboratory, but the above discussion must be regarded in the nature of surmise rather than as serious explanation.

The only records available concerning local field populations are woefully inadequate. The figures are given below for what they are worth (Table 7). If we may judge the age of the females from their weights, according to the relations previously found, the animals from Vredefort were born towards the end of July, and the beginning of August. The Zululand juveniles were probably born in March–April and the South

West African juveniles in April–May. The seasons here indicated for these widely scattered samples, could be similar to those found in Sierra Leone. The collections are inadequate, however, and a sudden decline in the rodent population of the Orange Free State made it impossible to continue collections started in September 1950.

The picture obtained from this study of *Rattus natalensis* is that of a species with a tremendous potential for increase which will be greatly affected by factors influencing the length of the breeding season, and great variations in the yearly abundance of the

Table 7. *Field collections of* Mastomys

Place of collection	Date	Number of specimens	Percentage adult	Percentage juvenile	Percentage pregnant	Percentage parous, non-pregnant
Zululand	May 1947	16	81	19	6	56
Vredefort (Orange Free State)	Sept. 1950	21	0	100	0	0
South West Africa	June and July 1951	204 (M. and F.)	3 (doubtful)	97	0·5	0

species are to be expected. A similar conclusion is given by Leslie & Ranson (1940) for the vole. We must, however, remember that these conclusions have been based on certain assumptions and generalizations, which may not apply to conditions in the field. Despite inadequacies, however, it is felt that this study gives some interesting evidence on the behaviour of the species and is so presented.

ACKNOWLEDGEMENTS

The author gratefully acknowledges his indebtedness to Mr P. H. Leslie for much valuable criticism and advice during the preparation of this report. I am also indebted to the Secretary for Health for permission to publish this paper.

SUMMARY

1. A life-table is given for female *Rattus natalensis* in the laboratory.

2. A fecundity-schedule for the female *R. natalensis* is provided.

3. The average productivity of the females was found to be 0·45518 litter and 3·33309 young per female per 28 days. The sex-ratio in the young born was 0·51909 female.

4. From the life-table and fecundity-schedule parameters have been derived. The intrinsic rate of natural increase was found to be 0·4068 per head per 28 days. The finite rate of natural increase was thus 1·502 per head per 28 days. The birth-rate was 0·5926 per head per 28 days and the death-rate was 0·1858 per head per 28 days.

5. Consideration is given to the possibility of a non-breeding season occurring in the field, and the effect this would have on the rate of natural increase of the population.

6. The population parameters are tentatively interpolated to apply to a field population, and the results are compared with the field results of other workers.

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STUDIES ON THE MICROCLIMATE OF *CALLUNA* HEATHLAND

By M. J. DELANY*

Department of Zoology, University College of the South West, Exeter

(With 117 Figures in the Text)

INTRODUCTION

This study has been undertaken with a view to determining the actual physical conditions under which an insect approximately 1 cm. long and inhabiting the base of *Calluna vulgaris* Salisb. lives. The measurements, made on various days in 1951 and 1952, constituted a portion of the author's research into the ecology of *Dilta littoralis* Wom. (Insecta, Thysanura). The microclimatic readings have been made within herbage up to 20 cm. high and thereby differing from the heathland study of Berg (1936) by being restricted to an extremely narrow stratum. Short notes by Champness (1950) and Waterhouse (1950) have appeared on the microclimates of grassland, and by Broadbent (1949) on potato crops. Apart from these, studies into the microclimate of a low plant cover are very sparse.

The procedure adopted in this study has been to compare the climates, as represented by temperature and humidity, close to the ground in and out of vegetation. The apparatus had to be accurate, portable and sufficiently small to enter the vegetation without disturbing its climate. A type F 1512/300 thermistor, incorporated in a bridge circuit similar to that designed by Penman & Long (1949) was used for measuring temperature. Relative humidity was determined using papers 0·5 cm. square impregnated with cobalt-thiocyanate as described by Solomon (1945). The temperature readings, using one thermistor, were made visually, half-hourly and the height above ground-level determined with a slender graduated stick. As the temperatures required were those experienced by the insect the thermistor was never shaded and was maintained with its long axis vertical to the substrate and the sensitive tip nearest the ground. Each cobalt-thiocyanate paper was pierced by an entomological pin which was then inserted into vegetation or ground so as to bring the sensitive paper in the required position. Care was taken, particularly when humidities were high, to ensure freedom from contact between the paper and any surrounding surface. Exposure was for 30 min. and the recorded times of readings are the mean of this half hour.

The measurements have all been made on Bicton Common, an area of heathland 300–400 ft. above sea-level, eight miles south-east of Exeter. The actual patches of *Calluna* in which measurements have been made have been selected as representing typical plants free from association with other species of both their own, e.g. *Erica*, and higher, e.g. *Ulex*, *Pinus* layers. Pioneer *Calluna* has been observed to assume two growth forms consisting of either a thick canopy close to the ground or the same with a more open, thinner layer above it. The thick canopy has subsequently been referred to as dense *Calluna*.

* Now at Dept. of Biology, University of Florida, Gainesville, Fla.

RESULTS

The results are recorded for selected days of readings, these being representative of the more extensive series made. Times are expressed in hours G.M.T., temperature in degrees Centigrade, and humidity in percentage relative humidity.

(*a*) *Measurements on 4 June 1952* (*Table 1*)

The temperatures of the two ground surfaces, within cover and of nearby open ground, show the base of vegetation to be cooler (Fig. 1) and less readily heated than that of open ground and so restricting the temperature range considerably. At higher levels above ground temperatures within the *Calluna*, approximate more closely to those above bare ground (Figs. 2, 3), this being due in general to temperature decreases above the open ground and increases within the *Calluna*.

Table 1. *Temperatures on 4 June 1952, 0900–1600 hr.*

(Height covered by profile, 15 cm.; maximum height of *Calluna*, 15 cm.—dense up to 10 cm.)

	Among vegetation		In the open		Difference,
	° C.	Time	° C.	Time	° C.
GROUND LEVEL					
Minimum	13·75	1200, 1600	15·8	1600	2·05
Maximum	18·8	0930	25·5	1030	6·7
Difference	5·05	—	9·7	—	—
0·5 CM. ABOVE GROUND					
Minimum	13·1	1600	13·1	1600	0·0
Maximum	18·5	0930	22·5	1030, 1330	4·0
Difference	5·4	—	9·4	—	—

The first profile readings (Fig. 5) show a temperature inversion. This is followed by cooling at the base of vegetation (although meanwhile the temperature of uncovered ground is increasing), and from then until 1500 hr. (Fig. 16) the profile pattern is one of greatest heat at the upper surface of the dense *Calluna*; above this it is generally cooler. At 1530 and 1600 hr. (Figs. 17, 18) the onset, with thermal decline, of temperature inversion appears.

The day was one of low humidities (Fig. 5) being only 45% R.H. at the base of the *Calluna* at 1900 hr. and rising to a maximum of 75% at 1600 hr. Over open ground at 1000 hr. the R.H. was 60%, 15% higher than at the base of *Calluna*, but of the remaining readings it was consistently lower rising from 40% at 1230 to 68% at 1600.

(*b*) *Measurements on 14 July 1951* (*Table 2*)

On this warm day of moderate humidities the open ground temperature underwent fluctuations which the base of the vegetation followed with less rapidity and intensity;

Figs. 1–20. Fig. 1. Temperatures at base of *Calluna* (—) and of open ground surface (---), 4 June 1952. Fig. 2. Temperatures 0·5 cm. above ground surface within *Calluna* (—) and over exposed ground (---), 4 June 1952. Fig. 3. Temperatures at upper surface of *Calluna* (—) and 5 cm. above open ground surface (---), 4 June 1952. Fig. 4. Humidities just above ground surface within *Calluna* (—) and over exposed ground (---), 4 June 1952. Figs. 5–18. Temperature profiles within *Calluna* (—) and over open ground (---) at the times stated (hr. G.M.T.), 4 June 1952. Fig. 19. Temperatures at base of *Calluna* (—) and of open ground surface (---), 14 July 1951. Fig. 20. Humidities within *Calluna* at 1 cm. (—), 4 cm. (. . .) and 7 cm. (---) above ground surface, 14 July 1951.

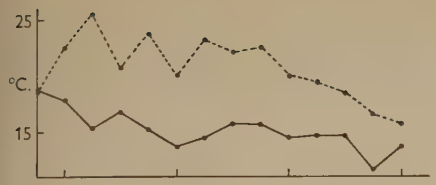


Fig. 1

Fig. 3

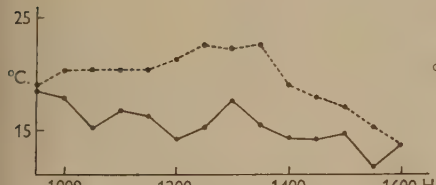


Fig. 2

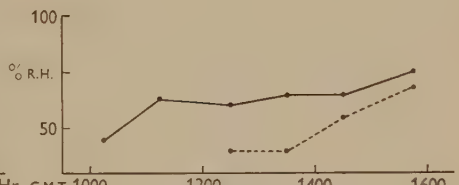


Fig. 4

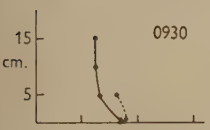


Fig. 5

Fig. 9

Fig. 13

Fig. 16

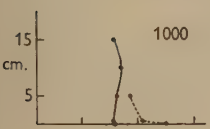


Fig. 6

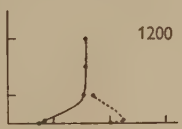


Fig. 10

Fig. 14

Fig. 17

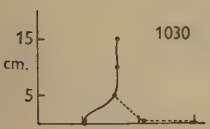


Fig. 7

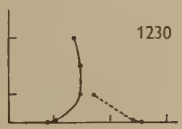


Fig. 11

Fig. 15

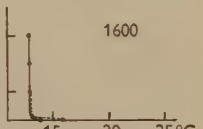


Fig. 18

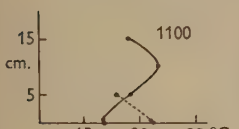


Fig. 8

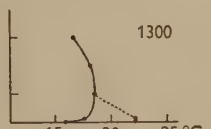


Fig. 12

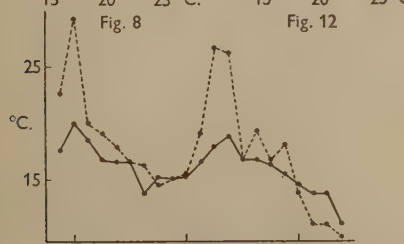


Fig. 19

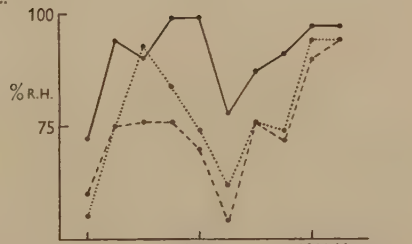


Fig. 20

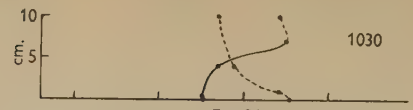


Fig. 21

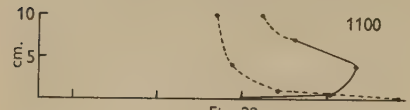


Fig. 22

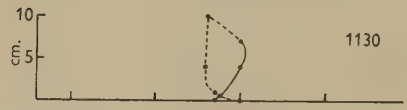


Fig. 23

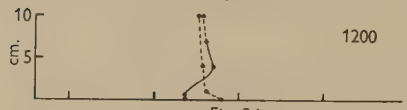


Fig. 24

Fig. 25

Fig. 26

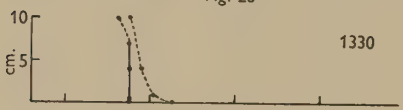


Fig. 27

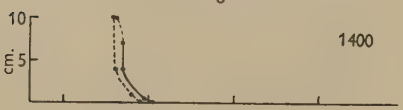
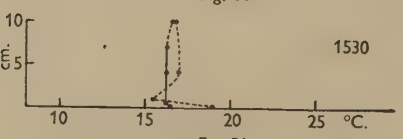


Fig. 28

Fig. 29

Fig. 30



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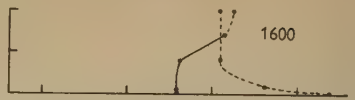


Fig. 32

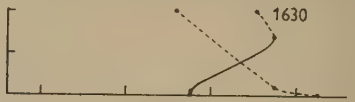


Fig. 33

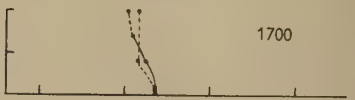


Fig. 34

Fig. 35

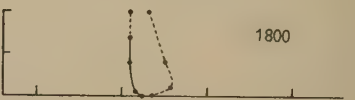


Fig. 36

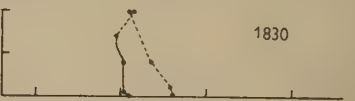


Fig. 37

Fig. 38

Fig. 39

Fig. 40

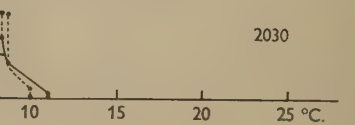


Fig. 41

Figs. 21–41. Temperatures within *Calluna* (—) and over open ground (---) at the times stated, 14 July 1951.

this is shown particularly by the temperature increases at 1100 and 1600 hr. (Fig. 19). The actual temperature range at the base of the vegetation was more than twice that of the open. The profiles in and out of the vegetation follow one another very closely,

Table 2. *Temperatures on 14 July 1951, 1030–2030 hr.*

(Height covered by profile, 10 cm.; maximum height of *Calluna*, 7 cm.—dense up to 7 cm.)

	Among vegetation		In the open		Difference,
	° C.	Time	° C.	Time	° C.
GROUND LEVEL					
Minimum	11	2030	9·9	2030	1·1
Maximum	20	1100	29·2	1100	9·2
Difference	9	—	19·3	—	—
4 CM. ABOVE GROUND					
Minimum	8·6	2030	8·6	2030	0·0
Maximum	26·8	1100	20·4	1530	6·4
Difference	18·2	—	11·8	—	—
10 CM. ABOVE GROUND					
Minimum	8·3	2030	8·6	2030	0·3
Maximum	22·7	1630	20·4	1600	2·3
Difference	14·4	—	11·8	—	—

the most obvious deviations occurring at the warmer periods (Figs. 21, 22, 32 and 33) and from 1130 to 1200 hr. (Figs. 23, 24) when they are of reverse forms. Between 1030 and 1630 hr. (Figs. 21–33) the temperature of the upper surface of the *Calluna*, with exceptions at 1500 and 1530 hr. (Figs. 30, 31), were higher than 3 cm. above it; at the same height over open ground temperatures are usually slightly higher than at the surface of the *Calluna*.

Table 3. *Temperatures on 14 July 1952, 1000–1530 hr.*

(Height covered by profile, 10 cm.; maximum height of *Calluna*, 14 cm.—dense up to 14 cm.)

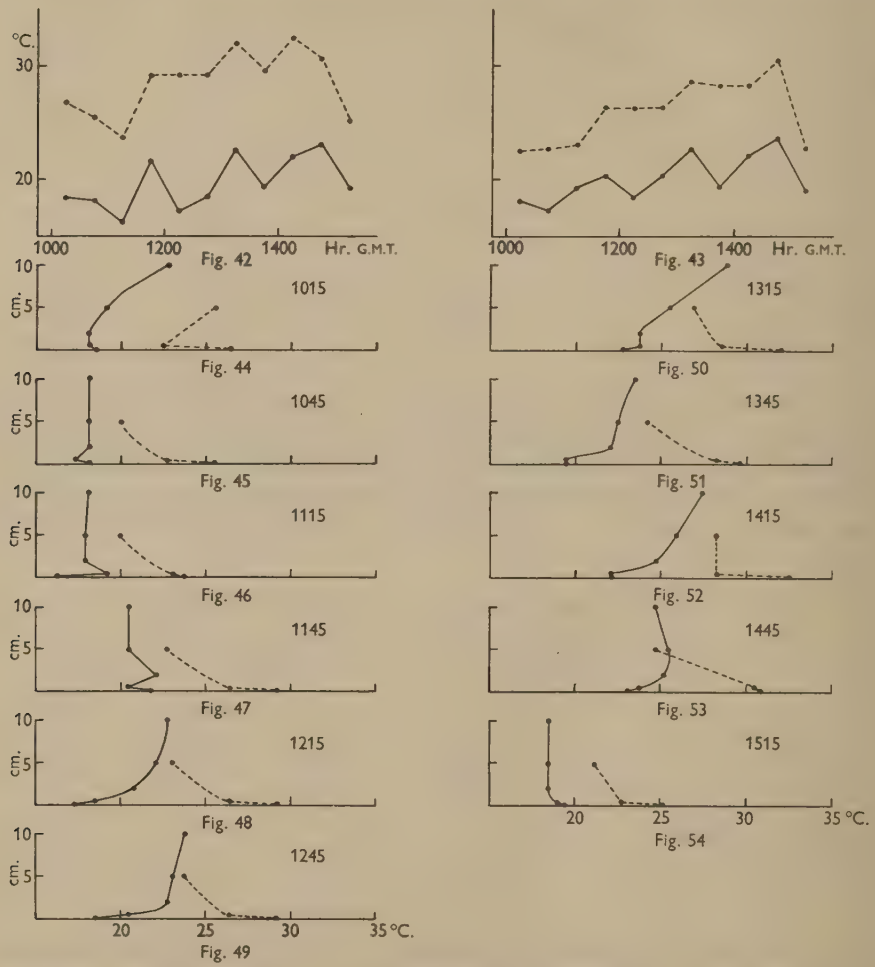
	Among vegetation		In the open		Difference,
	° C.	Time	° C.	Time	° C.
GROUND LEVEL					
Minimum	16·3	1115	23·7	1115	7·4
Maximum	23·1	1445	32·5	1415	9·4
Difference	6·8	—	8·8	—	—
0·5 CM. ABOVE GROUND					
Minimum	17·3	1045	22·5	1015	5·2
Maximum	23·7	1315, 1445	30·5	1445	7·2
Difference	6·4	—	8·0	—	—

Humidity was at its lowest at 1100 and 1600 hr., when the warm spells prevailed, and decreased as the vegetation was ascended.

(*c*) *Measurements on 14 July 1952* (*Table 3*)

On this day measurements were made for only a short period. The temperature at the base of the *Calluna* is, in common with the preceding measurements, lower than that of open ground. The features of note are the magnitude and large degree of temperature fluctuation of both ground surfaces (Fig. 42). At 0·5 cm. (Fig. 43) the temperatures within the vegetation have increased and the open ones decreased. The

profiles between 1045 and 1145 (Figs. 45–47) have a fluctuating basal temperature with the air immediately above lagging behind it. From then onwards (Figs. 48–53) there follows the more usual form of a cool base, temperature rising rapidly as the vegetation is ascended. The external temperature displays a reverse relation to that in the vegetation.



Figs. 42–54. Fig. 42. Temperatures at base of *Calluna* (—) and of open ground surface (---), 14 July 1952. Fig. 43. Temperatures 0·5 cm. above ground surface within *Calluna* (–) and over exposed ground (---), 14 July 1952. Figs. 44–54. Temperature profiles within *Calluna* (—) and over open ground (---) at the times stated (hr. G.M.T.), 14 July 1952.

(*d*) *Measurements on 21–22 July 1951* (*Tables 4 and 5*)

This period was noteworthy for the persistence of high humidities, due partly to heavy rain between 0430 and 0630 hr. and 1330 and 1430 hr. Unlike any of the other periods investigated this was undertaken over a 24 hr. period, and for the convenience

Table 4. *Temperatures during the hours of full light on 22 July 1951*

(Height covered by profile, 12 cm.; maximum height of *Calluna*, 7 cm.—dense up to 7 cm.)

GROUND LEVEL, 0900–1900 hr.

	Among vegetation		In the open		Difference,
	° C.	Time	° C.	Time	° C.
Minimum	18·5	1500	17·3	0800, 0830, 1730	1·2
Maximum	24·25	1230	23·7	1230	1·45
Difference	5·75	—	6·4	—	—

ABOVE GROUND, 0800–1800 hr.

	5 cm. above surface of *Calluna*		5 cm. above open ground		Difference,
	° C.	Time	° C.	Time	° C.
Minimum	15·8	1800	16·3	1800	0·5
Maximum	22·5	1130	23·7	1200	1·2
Difference	6·7	—	7·9	—	—

of comparison the maximum and minimum temperatures have been displayed in two groups. Table 4 covers the hours of daylight, and Table 5 those of darkness and failing light.

In comparing the ground temperatures (Fig. 55) it is evident that the variation is only slight, the data suggesting a higher temperature maintained within narrower

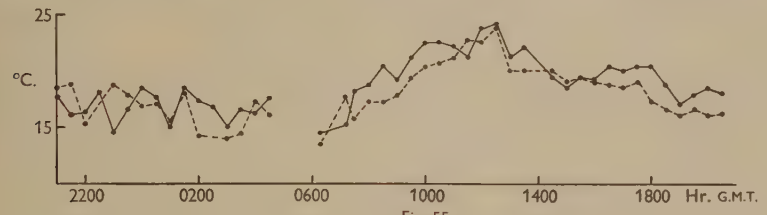


Fig. 55

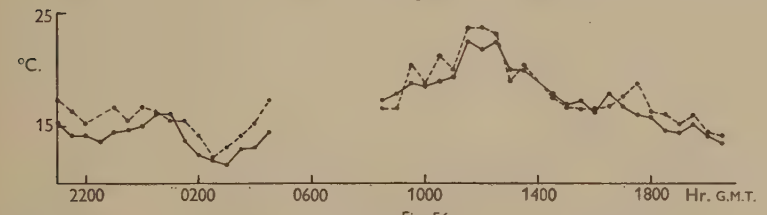


Fig. 56

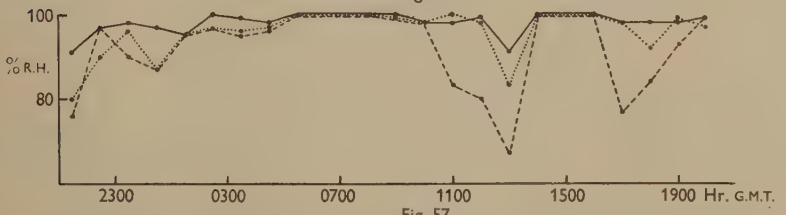
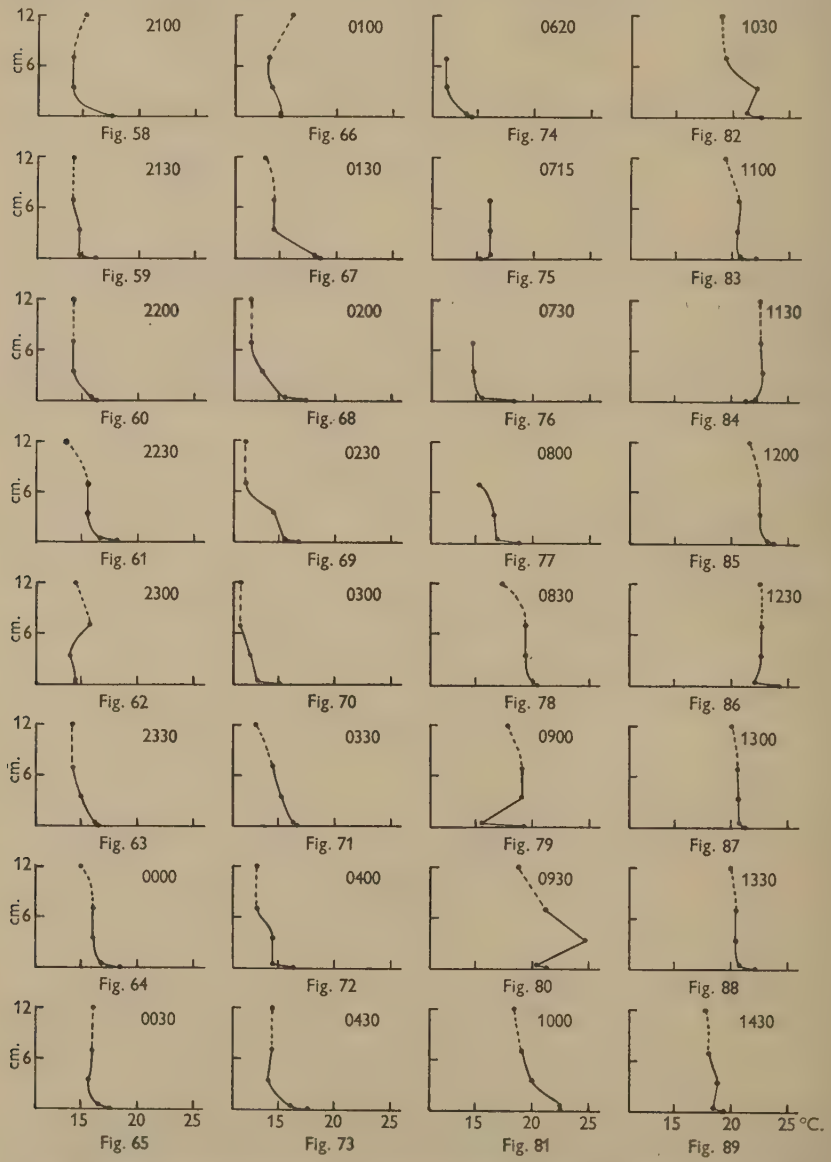


Fig. 57

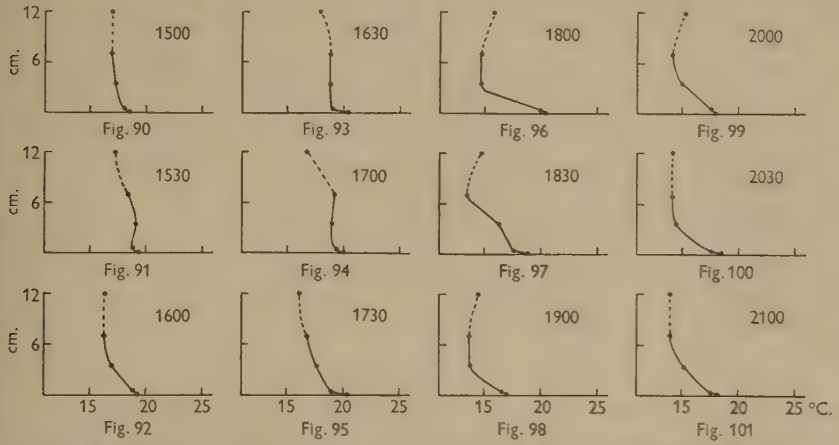
Figs. 55–57. Fig. 55. Temperatures at base of *Calluna* (—) and of open ground surface (- - -), 21–22 July 1951. Fig. 56. Temperatures 5 cm. above top of *Calluna* (—) and 5 cm. over open ground (- - -), 21–22 July 1951. Fig. 57. Humidities within *Calluna* at 1 cm. (—), 4 cm. (. . . .) and 7 cm. (- - -) above ground surface, 21–22 July 1951.

limits at the base of the vegetation. The narrowness of these limits is apparent when it is considered for the 24 hr. period, since all the ground temperatures lay between 13·5 and 24·25° C. The temperature differences 5 cm. above ground and 5 cm. above vegetation (Fig. 56) indicate it to be cooler over the vegetation, in all but six of the forty-three measurements. The majority of the temperature profiles (Figs. 58–101)



Figs. 58–89. Temperatures within (—) and immediately above (---) *Calluna* at the times stated (hr. G.M.T.), 21–22 July 1951.

conform to a common pattern affected little by time of day and humidity. As the vegetation is ascended cooling takes place, although its magnitude and the stratum most affected are variable. Figs. 79 and 80 display unusual configurations. In both, the temperature at ground-level is the same as the upper vegetation surface with



Figs. 90–101. Temperatures within (—) and immediately above (---) *Calluna* at the times stated (hr. G.M.T.), 21–22 July 1951.

a digression of 4° C. within the profile. Between 1100 and 1330 (Figs. 83–88) the degree of temperature inversion is reduced with the production at 1130 (Fig. 84) of a more conventional profile.

The humidities were distinctly high, never dropping below 90% R.H. at the base of the *Calluna*, whilst at its upper surface the lowest record was 67% R.H.

Table 5. *Temperatures during the hours of darkness and failing light (2100–0730 and 1830–2030 hr.) on 21–22 July 1951*

(Height covered by profile, 12 cm.; maximum height of *Calluna*, 7 cm.—dense up to 7 cm.)

GROUND LEVEL

	Among vegetation		In the open		Difference,
	° C.	Time	° C.	Time	° C.
Minimum	14·5	2300	13·5	0620	1·0
Maximum	18·8	1830	18·8	2130, 2300	0·0
Difference	4·3	—	5·3	—	—

ABOVE GROUND

	5 cm. above surface of *Calluna*		5 cm. above open ground		Difference,
	° C.	Time	° C.	Time	° C.
Minimum	13·0	0330	12·0	0620	1·0
Maximum	16·1	0030, 0100	17·3	2100, 0430	1·2
Difference	3·1	—	5·3	—	—

(*e*) *Measurements on 4 December 1951* (*Table 6*)

On this cool winter day the base of the *Calluna* displayed a more even temperature (Fig. 102), and with approaching darkness cooled more slowly than did the open ground, which eventually became actually the colder of the two. The profiles

(Figs. 103–117) conform to a uniform pattern, having their major temperature increases between 3 and 5 cm., and it is only during the two rather warmer periods at 1045 (Fig. 104) and 1145 hr. (Fig. 106) that a difference between the ground surfaces of more than 3·5° C. occurs.

Table 6. *Temperatures on 4 December 1951, 1015–1700 hr.*

(Height covered by profile, 15 cm.; maximum height of *Calluna*, 20 cm.—dense up to 10 cm.)

	Among vegetation		In the open		Difference,
	° C.	Time	° C.	Time	° C.
GROUND LEVEL					
Minimum	3·1	1545	2·8	1700	0·3
Maximum	8·4	1015	13·8	1045	5·4
Difference	5·3	—	11·0	—	—
0·5 cm. ABOVE GROUND					
Minimum	3·0	1545	3·3	1700	0·3
Maximum	8·3	1045	12·7	1045	4·7
Difference	5·3	—	9·4	—	—

DISCUSSION

Certain difficulties present themselves, particularly the variations in time, in comparing the temperature and humidity figures. In Table 7 the ground temperature in and out of *Calluna* for similar time periods (1000 to 1530 hr.) are displayed. These figures cover the warmest portions of the day and show two features, the narrower temperature range at the base of the vegetation, and the tendency for comparable temperatures to be lower in the *Calluna*. The only exception to the latter is the slightly higher

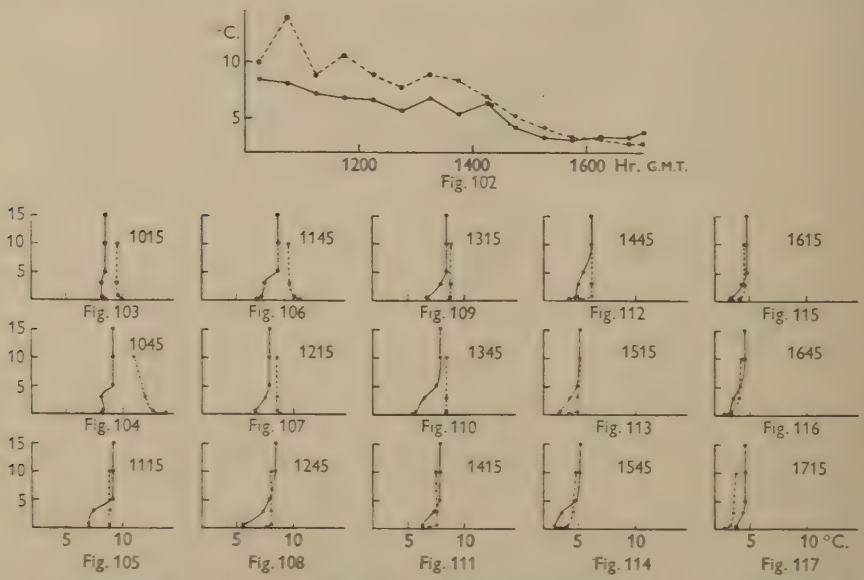


Fig. 102. Temperatures at base of *Calluna* (—) and of open ground surface (---), 4 December 1951.
Figs. 103–117. Temperature profiles within *Calluna* (—) and over open ground (---) at the times stated (hr. G.M.T.), 4 December 1951.

maximum in *Calluna* on 22 July when the range of the exposed ground was unusually low. Although these figures have been taken from dense *Calluna* from 7 to 14 cm. high, the salient features are sufficiently distinct to be considered irrespective of this. Within the vegetation the maximum experienced was 24·25° C., whilst outside it temperatures ranging between this and 32·5° C. were not infrequent. These surface soil maxima are appreciably lower than those of 50–60° C. found by Vaartaja (1949) on heathland in Finland.

Outside the times covered by Table 7 comparisons indicate during the hours of darkness on 21–22 July a close approach to one another (Table 5) and with the approach of darkness on 4 December and 14 July 1951 a slightly lower temperature outside the *Calluna*. The temperature profiles within *Calluna* generally assume one of two forms; having either a warmer base than upper surface or vice versa with the maximum temperature change occurring within the first 3 cm. In addition, and less frequently, there appears the more uniform pattern of little vertical variation.

On a warm day of low humidities (4 June) the profile was commonly found to be of the second type displaying an increase of 2–4° C. within 10 cm. This profile pattern is followed on 14 July 1952 (Figs. 48–52) and 4 December (Figs. 104–117) where the

Table 7. *Temperature maxima and minima between 1015 and 1515 hr.*

	Base of *Calluna*			Open ground		
	Min.	Max.	Range	Min.	Max.	Range
4 June 1952	13·75	16·8	3·05	18·5	25·5	6·0
14 July 1951	13·75	20·0	6·25	15·0	29·2	14·2
14 July 1952	16·3	23·1	6·8	23·7	32·5	9·8
22 July 1951	18·5	24·25	4·75	19·0	23·7	4·7
4 Dec. 1951	3·3	6·8	3·5	4·1	13·8	9·7

increases are between 4·5 and 6° C. in July and around 2° C. in December. An inverse relationship occurred over open ground on the summer days, with a rapid temperature decline just above its surface. On 14 July 1951, when humidities were moderate, the temperature reached within the vegetation differed little except during the warm spells (Figs. 21, 22, 32 and 33) from that of uncovered ground, variation within a profile being only of the order of 2° C. The effect of temporary increases of incoming radiation appears only to heat the open ground and the upper layers of the herbage (Figs. 32, 33). The general form throughout 21–22 July is one of inverse profiles displaying accentuation during the night and hours of daylight when incoming radiation is lowest. The persistence of this inverse relation is apparently partly due to rain from 0430 to 0630 hr. and 1330 to 1430 hr. tending to produce more even temperatures.

Geiger (1950), in his work on antirrhinum and rye plants growing up to 175 cm., found the profile form at times of incoming radiation to be dependent upon the growth-form of the plant. In both types of cover provided by these plants the maximum difference between highest and lowest temperatures at midday was 4° C., this occurring in plant cover 80 cm. high. In this study on the *Calluna* microclimate variations of this order have not been uncommon on warm days. When it is considered that the dense herbage never exceeded 14 cm., the temperature gradients within it must be

considered sharper than those found by Geiger. On the other hand, the *Calluna* temperatures are of note for their lack of conformity. Not only is the magnitude of temperature range subject to appreciable variation over short periods but so also is the profile form. Whilst the base of the vegetation is usually either the warmest or coolest portion of the profile, the transference from one to another of these forms may be effected within as short a period as one hour (Figs. 5 and 7).

Some interesting temperature measurements have been made in the tropics by Ramdas, Kalamkar & Gadre (1934) in sugar-cane and millet. Their figures are means of a number of readings. According to the crop there may occur at midday from the base either an increase of 6° C. in sugar-cane of 250 cm., or a drop of 2° C. in millet 180 cm. high. Similar changes have been observed in *Calluna* (Figs. 49, 88) during the warmer periods of the day, thereby substantiating the diversity of temperature gradients which may be experienced in this plant cover. It is maintained by Geiger and Ramdas *et al.* that for a given time of day and year the temperature pattern within a plant cover is conditioned largely by the physical form of the constituent plants. It appears that the case is far from being so simple in low *Calluna*. On 21–22 July the high precipitation and generally humid atmosphere appear to have had a considerable levelling effect upon temperature. Furthermore, when humidities were known to be lowest (4 June) temperature differences between open ground and the base of vegetation were greatest. It is also of note that the base of the vegetation is of quite different composition to the open ground; the former consisting of the A_0 horizon of leaf litter is more water retentive than the soil of exposed ground. From these data it appears that temperature in a low, closely packed plant layer can be appreciably influenced by moisture due either to direct precipitation or to the water retaining power of the humus layer at its base.

It is not within the scope of this paper to analyse in detail the factors responsible for maintaining the microclimate, and it would require many more readings before this could be adequately done. This is brought out by the appearance of a number of anomalous readings, e.g. Figs. 6 and 7, where the profiles acquire most unorthodox configurations, and Figs. 47, 79 and 80, where the temperature of open ground is increasing and that beneath *Calluna* decreasing. The major object has been to deduce, as far as possible, by comparing it with that of uncovered ground, the climate in which *Dilta littoralis* lives. The effect of insolation, the factor responsible for greatest temperature fluctuation, on warmer days is appreciably reduced by the vegetation, resulting in a cooler more equable climate at its base. Humidities have been found to be highest at the base of the *Calluna*, and to decline as it has been ascended and although fairly low values have occurred in the *Calluna* it is possible that they are only of short duration. Fluctuations in temperature and humidity undoubtedly occur in this habitat, their intensity being determined by, but never as great as, the climate outside the plant cover.

ACKNOWLEDGEMENTS

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SUMMARY

1. Measurements of temperature and humidity have been made within *Calluna* up to 20 cm. high and over adjacent ground uncovered by vegetation on five days of differing climatic conditions.

2. During daylight ground surface temperatures were generally cooler and more even within vegetation than in the open.

3. The form of the temperature profile within *Calluna* has varied considerably from day to day and within short periods of the same day.

4. Humidities tended to be highest and least variable at the base of the vegetation.

5. The overall effect of the vegetation was to produce a more equable climate at its base.

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OBSERVATIONS ON THE EPIFAUNA OF THE DEEP-WATER MUDS OF THE CLYDE SEA AREA, WITH SPECIAL REFERENCE TO *CHLAMYS SEPTEMRADIATA* (MÜLLER)

By J. A. ALLEN

Zoology Department, The University, Glasgow, and the Marine Station, Millport

(With 11 Figures in the Text)

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INTRODUCTION

In the sublittoral survey of the Clyde Sea Area from 1949 onwards it became evident that there is an epifaunal association on the deep-water muds of this area consisting mainly of animals living on the shells of molluscs, particularly *Chlamys septemradiata*. It also appeared that this deep-water mud epifauna differed in different regions of the Clyde, and that the populations of *C. septemradiata* themselves differed somewhat. A series of samples were taken in 1951 over a period of seven months (May to December) from different parts of the area. Over 2200 shells were examined and the results analysed. These not only gave details of the epifauna as a whole, but also gave information on the length of life and growth-rate of *C. septemradiata* and some of the attached animals.

The most detailed work on epifauna is that of Gislén (1930). He made a detailed study of Gullmar Fjord and refers to 'epibioses' as he considers both the flora and the fauna. He points out that Petersen's division of infauna and epifauna as corresponding to soft and hard bottoms respectively is not entirely true, and that there is an epifauna of soft bottoms and an infauna of hard bottoms. Thus epibioses are described as biocoenoses of animals and plants which occur entirely above the bottom surface or only have an anchoring organ in the bottom.

On soft bottoms in deep water Gislén recognizes three associations; a *Pennatula* association with no other epifaunal species, a *Virgularia* association with *Cerianthus lloydi* Gosse and *Bougainvillea ramosa* Allman, the latter being found on the naked

tip of the shafts of *Virgularia*, and a *Funiculina* association. Korringa (1951) has carried out similar studies to the present, and has described the epifauna of *Ostrea edulis* L. in detail. This work will be discussed further below.

DEEP-WATER MUD EPIFAUNA

With the exception of that associated with shells the only epifauna present on the deep-water muds within the Clyde Sea Area is the *Pennatula* and *Virgularia* associations of Gislén. These occur together and as far as these results show, they need not be separated into distinct associations. *Pennatula phosphorea* L. is the dominant species, and both are widely distributed on the deep-water muds. *Pennatula* was found to be the dominant species of the whole fauna (including infauna) of the Plateau, the area at the mouth of the Firth around Ailsa Craig (Fig. 1). No specimens of *Bougainvillea* or other hydroids were found attached to the *Virgularia*. *Cerianthus lloydi* was found in the Cumbrae Deep associated with the species above, but it does not appear to be so widely distributed as these. The *Funiculina* association was not discovered in the Clyde.

With the exception of Gislén, workers on sublittoral faunas have always included species of *Chlamys* and *Pecten* in the lists of infaunas. Both Petersen (1918) and Spärck (1935) refer *Chlamys septemradiata* to the *Haploops* community, while they name the infaunal community from depths below 200 m. in the Skagerrak as the *Chlamys* (*Pecten*) *vitrea* (Chemnitz) community. From the definition of Gislén (accepted here) not one of these species can be referred to the infauna. The following species are to be found in the Clyde Sea Area: *Pecten maximus* (L.) and *Chlamys distorta* (da Costa) on hard bottoms in deep water; *C. opercularis* is widely distributed throughout the area as are *C. similis* (Laskey), *C. striata* (Müller) and *C. tigerina* (Müller), although the latter three species are rarely found on deep-water muds; *C. varia* (L.) is found on hard bottoms in shallow water; *C. septemradiata* is only found on deep-water muds.

C. varia, *C. opercularis*, *C. septemradiata* and *Pecten maximus* are usually found with epifauna on the upper valve. All except *C. septemradiata* have species of epifaunal animals that are present on the substratum on which they live. It was found that *C. septemradiata* does not occur in the Sound of Jura and the lochs from West Loch Tarbert to Loch Craignish, its place being taken by *C. opercularis*, which is very common on all types of bottom in this area and always carries a large amount of epifauna on its upper valve.

THE SHELL AS A HABITAT

Apart from the Pectinidae, many molluscs that live on the surface of the substratum provide surface for attachment. If these shells are present in large numbers a definite community such as the *Mytilus* and *Modiolus* associations may be formed. Such a community may support species that are almost entirely peculiar to it such as *Capulus* on the *Modiolus* shells. Korringa (1951), in a study on the epifauna of *Ostrea edulis*, points out that the oyster beds form a specialized habitat for a very rich fauna and that this fauna is noticeably different from that of the surrounding bottom of the district.

Apart from *Chlamys septemradiata* the only other molluscs from deep-water muds

that have epifaunal organisms attached are *Buccinum undatum* L., *Neptunea antiqua* (L.) and *Nucula sulcata* Bronn. *Chlamys opercularis* is not very common on these grounds, and the few specimens that have been taken have no epifauna. Most of the *Buccinum* and *Neptunea* had no epifauna, and those that did had the same species that were on *Chlamys septemradiata*. *Nucula sulcata*, which is part of the infauna, was found to be the substratum for *Perigonimus repens* (Wright). This was found attached to the ventral surface in 78·5% of the shells examined.

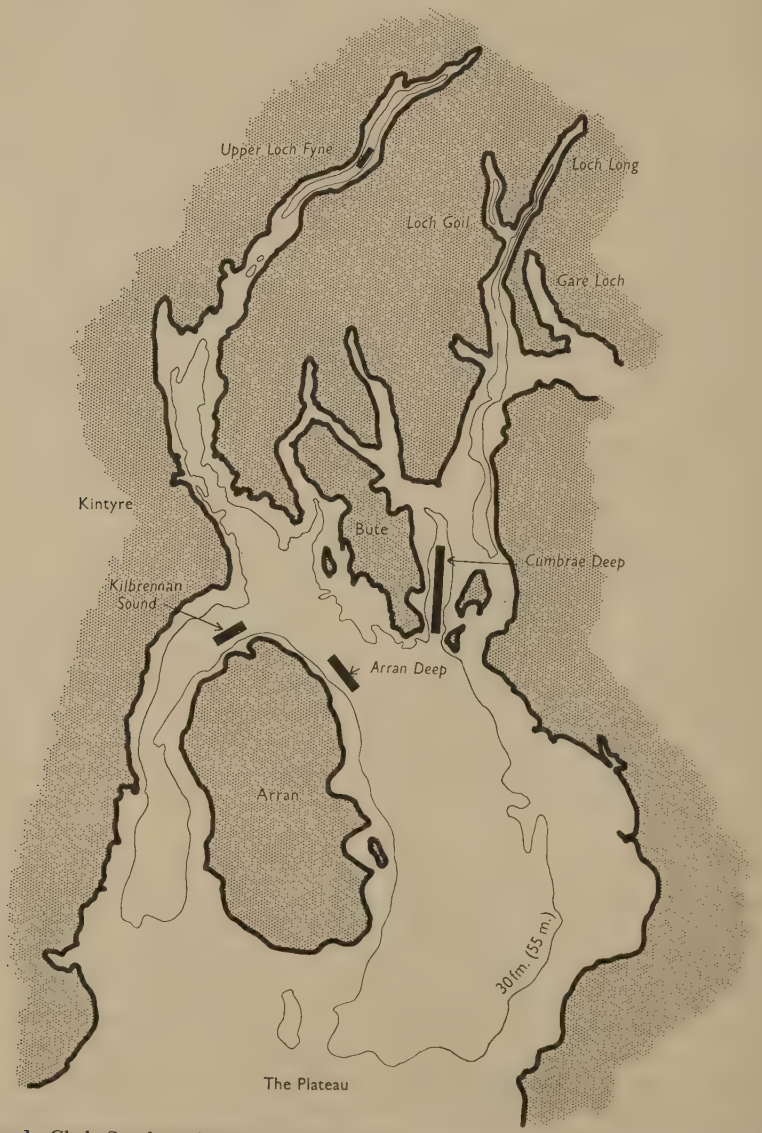

Fig. 1. Clyde Sea Area showing the four localities sampled and the 30-fathom (55 m.) line.

Apart from the mud itself and a very few rocks, the only substratum for the attachment of the epifauna is that afforded by other animals, particularly the molluscs. Much of this mud is floccular, and because of this the epifauna must be raised some distance above the surface of the mud if it is to avoid silting. Thus *Chlamys septemradiata*, which presumably moves about on the surface of the mud, forms an ideal substratum. *Buccinum* and *Neptunea* are not so suitable as they move within the top layers of the mud and therefore any attached animals are liable to become silted up. In addition, the flapping of the valves in *Chlamys septemradiata* will keep the shell surface free from silt. Korringa points out that in addition to the shelter afforded by the oysters there is the important factor of protection from silting, for the oyster, although sessile, manages to keep free from silt. He also points out that although there is no evidence to show that the faeces and the pseudofaeces do contribute to the food of the epifauna, they may well do so. Similarly, the faeces and pseudofaeces may be a source of food for the epifauna of *C. septemradiata*. The length of life of the epifaunal organisms is limited to the length of life of the *C. septemradiata*. The only epifaunal animal that was taken alive from a dead *Chlamys* shell was *Sabella pavonina* Savigny. Once attached, the *Sabella* can build a tube that will stand above the surface of the bottom. The lack of epifauna on dead shells indicates that the problem of silting is of great importance.

CHLAMYS SEPTEMRADIATA

C. septemradiata is generally distributed within the Clyde Sea Area on deep-water muds (70 m. and below). It was found in fairly large numbers in four localities, and these were sampled with the Agassiz trawl. The areas sampled were the Cumbrae Deep, Arran Deep, Kilbrennan Sound and Upper Loch Fyne (see Fig. 1). Forbes & Hanley (1853) state that it is distributed from Scandinavia to the Mediterranean. In British waters it is listed from the Clyde and the west coast of Scotland. It is not listed for the Isle of Man, and as it was not taken from the Sound of Jura it is possible that the Clyde fauna is self-contained. It is associated with the following *infaunal* animals in all the localities sampled: Annelida: *Glycera rouxi* Audouin & Edwards, *Lipobranchius jeffreysii* (McIntosh); Mollusca: *Nucula turgida* Leckenby & Marshall, *N. sulcata*, *Abra alba* Wood, *Corbula gibba* (Olivi), *Cuspidaria cuspidata* Brown; Echinoidea: *Brissopsis lyrifera* (Forbes). At the south end of Cumbrae Deep it is associated with a small *Haploops* patch and in the Kilbrennan Sound there is a dominant population of *Nuculana minuta* (Müller).

(*a*) *Shell characteristics*

No colour differences were noted between the shells from the four localities sampled. There is individual variation in colour. This is basically brick red with a variety of mottled markings. The albino variety, which is recorded by Forbes & Hanley and by Jeffreys (1869), was taken from the Kilbrennan Sound and the Cumbrae Deep, and represents 0·4% of the total number of shells examined. Both valves of the youngest specimens taken were coloured brown and, although there is a gradual reduction of this colour on the lower valve (right), every shell up to 17 mm. in height (hinge—free margin, see Fig. 2*a*) was coloured on each valve. After this, the brown colour of the

lower valve disappears and all the shells of greater height than 28 mm. had a white under-surface and this was always discoloured by a deposit of manganese. This deposit was noted by Chumley (1918), and is to be found on many shells throughout the Clyde. Other species particularly affected are *Nucula nucleus* L., *N. sulcata*, *Astarte sulcata* (da Costa) and *A. montagui* (Dillwyn).

The shell of *Chlamys septemradiata* is very thin when compared with other species of *Chlamys*. Weight-per-unit-area was calculated for shells of various species, all shells were approximately 4 cm. in height and their areas varied from 11·5 to 13·9 cm.^{2}:

	Weight (g.)/unit area
Pecten maximus	1·77
Chlamys opercularis	1·94
C. varia	1·46
C. distorta	1·87
C. septemradiata	1·02

This is no doubt correlated with the mode of life as *C. septemradiata* probably swims more than the species living on hard bottoms in order to prevent itself sinking in the mud.

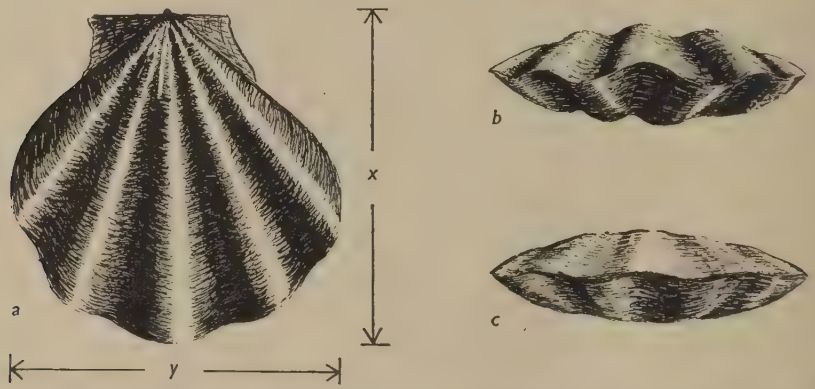

Fig. 2. *Chlamys septemradiata*. (*a*) View of upper valve showing the measurements taken, *X* hinge—free margin, *Y* antero-posterior. (*b*) Deep undulations of the Cumbrae and Arran Deep shells. (*c*) Slight undulations of the Kilbrennan Sound and Upper Loch Fyne shells.

The shell outline appears to be constant. Antero-posterior and hinge—free margin measurements were taken, and comparisons made between the age-groups and the localities sampled (see Fig. 2*a* and Table 1). The differences between the two measurements were compared. There is some tendency for the difference in the two measurements to get greater with age, and there are slight differences between the four localities. The ears, which vary in shape from species to species, are constant in shape for *C. septemradiata* and did not vary in the localities sampled. However, shell ribs do show differences both according to age and the locality from which the shell was taken.

The number of ribs varied from four to ten and, except close to the umbones, take the form of undulations. These undulations in the Cumbrae and Arran Deep samples are well marked with a large amplitude in the majority of cases. The Kilbrennan Sound and the Upper Loch Fyne samples have, in the main, shallow undulations, some of which are barely perceptible (Fig. 2*b*, *c*). In a mature specimen there are five main

ribs arranged symmetrically as in Fig. 2*a*, the median rib being most pronounced. Additional ribs are usually less pronounced than these five, and may not run completely from the umbo to the free margin. In the six- and seven-ribbed shells the additional ribs are to be found on the anterior side of the median rib, only occasionally

Table 1. *Average differences between the antero-posterior and hinge—free margin measurements of* Chlamys septemradiata *from four localities*

(Measurements in mm.; numbers of shells measured in parentheses)

Age-group	Cumbrae Deep	Arran Deep	Kilbrennan Sound	Upper Loch Fyne
I <11 mm.	—	—	0·84 (30)	—
II 12–24 mm.	0·74 (46)	0·89 (7)	1·20 (348)	0·97 (18)
III 25–39 mm.	0·56 (186)	1·18 (60)	1·10 (1348)	0·87 (217)
IV >40 mm.	0·82 (26)	1·60 (2)	—	—

(on 0·44% of the six-ribbed and on 1·76% of the seven-ribbed shells taken) is one of these ribs on the posterior side. No shell with seven ribs was found with both additional ribs on the posterior side. Similarly, specimens with eight ribs had never more than one of the additional ribs on the posterior side and this one posterior additional rib was present in 76·77% of the shells examined. Where nine and ten ribs

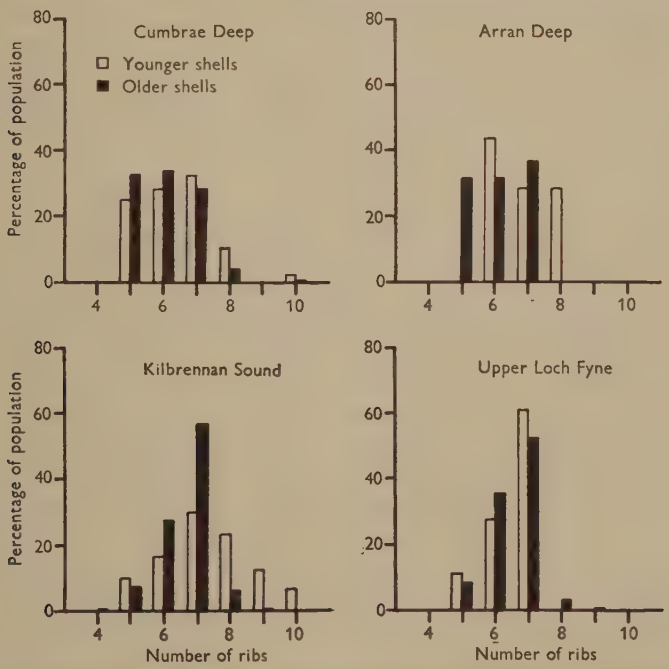

Fig. 3. Populations of *Chlamys septemradiata* arranged by rib-numbers and age-groups.

were present all cases, except one which had only one of its additional ribs on the posterior side, had two of the additional ribs on the posterior side.

There appears to be a reduction in the number of ribs as the shell gets older, this is clear from Fig. 3 and Table 2. This shows that the percentage composition of the

number of ribs in the four age-groups shifts from a high number of ribs in the first group to a low number in the fourth group. This is because some ribs may be laid down only for a short distance. In addition, there is a difference in the Cumbrae and Arran Deep populations and the Kilbrennan Sound and Upper Loch Fyne populations

Table 2. *Populations of* Chlamys septemradiata *classified by age-groups and by the number of ribs on the shell*

(Numbers of shells; percentages in parentheses.)

Ribs	Age-groups I	II	III	IV	Total Sample
			Cumbrae Deep		
4	—	—	—	—	—
5	—	12 (26·1)	68 (36·6)	8 (30·8)	88 (32·8)
6	—	13 (28·3)	71 (38·1)	7 (26·9)	91 (34·0)
7	—	15 (32·6)	42 (22·6)	10 (38·5)	77 (28·7)
8	—	5 (10·9)	5 (2·7)	1 (3·8)	11 (4·1)
9	—	—	—	—	—
10	—	1 (2·1)	—	—	1 (0·4)
Total	—	46	186	26	286
			Arran Deep		
4	—	—	—	—	—
5	—	—	19 (31·6)	—	19 (27·6)
6	—	3 (42·8)	19 (31·6)	1 (50·0)	23 (33·3)
7	—	2 (28·6)	22 (36·8)	1 (50·0)	25 (36·2)
8	—	2 (28·6)	—	—	2 (2·9)
9	—	—	—	—	—
10	—	—	—	—	—
Total	—	7	60	2	69
			Kilbrennan Sound		
4	—	—	1 (0·1)	—	1 (0·1)
5	3 (10·0)	28 (8·0)	96 (7·1)	—	127 (7·4)
6	5 (16·7)	83 (23·9)	396 (29·4)	—	484 (28·1)
7	9 (30·0)	186 (53·4)	767 (57·0)	—	962 (55·8)
8	7 (23·3)	43 (12·4)	82 (6·1)	—	132 (7·6)
9	4 (13·3)	7 (2·0)	4 (0·3)	—	15 (0·8)
10	2 (6·7)	1 (0·3)	—	—	3 (0·2)
Total	30	348	1345	—	1723
			Upper Loch Fyne		
4	—	—	—	—	—
5	—	2 (11·1)	18 (8·3)	—	20 (8·5)
6	—	5 (27·8)	77 (35·5)	—	82 (34·9)
7	—	11 (61·1)	14 (52·5)	—	125 (53·2)
8	—	—	7 (3·2)	—	7 (3·0)
9	—	—	1 (0·5)	—	1 (0·4)
10	—	—	—	—	—
Total	—	18	217	—	235

(see Table 2). The latter show that the seven-ribbed shell is the most common, comprising over 50% of the total population, while the five-ribbed shell represents about 8% of the total population. In the Arran Deep and Cumbrae Deep populations the five-, six- and seven-ribbed shells are in approximately equal numbers, each representing about 30% of the population.

(*b*) *Age and growth*

It can be seen from Fig. 4 that the shell measurements (hinge to free margin) fall into four size-groups: I, 4–11 mm.; II, 12–24 mm.; III, 25–39 mm.; and IV, 40–47 mm. These measurements apply to all samples taken from May to December, even though some growth has taken place between these dates. Although complete proof is lacking it is highly probable that these are year-groups, particularly when these results are correlated with those from the study of the epifauna.

Group I formed 1·3% of the total number of shells examined. They were taken from Kilbrennan Sound only and on both occasions that this area was sampled. On 3 August 1951, 13 specimens were taken and on 14 December 1951, 17 were taken. The size of the first sample ranged from 4 to 7 mm. in height, with an average of 5·5 mm. The range of the second sample was 5–11 mm., with an average of 8·4 mm. Thus from August to December the average height of the shell increased by 2·9 mm.

Group II shells were present in all but two of the samples and formed 18·3% of the total number of shells. The two samples from which this group was absent were those with the smallest number of shells, viz. 11 and 19 from the Cumbrae and Arran Deeps respectively. The samples taken from the Cumbrae Deep and the Kilbrennan Sound show a similar increase in the average height to group I over the same period. The Cumbrae Deep samples show an increase from 17 to 20·5 mm. and the Kilbrennan Sound from 18·7 to 20·4 mm.

Group III is by far the largest, forming 79·2% of all the shells taken, and is present in all samples. These shells show no significant increase in height from July to December.

Group IV shells are present only in samples from the Arran and Cumbrae Deeps. No shells over 39 mm. were present in the very large samples from other stations. 66·1% of this group was taken in June and July and there was no significant increase in size between June and November.

It has been pointed out already (p. 244) that the shell outline appears to be a constant shape throughout life. The shell increment between each age-group does not remain constant but increases in the first three. Thorsen (1946) reports that the spat settle in October in the Kattegat and that the prodissoconch is approximately 275μ in length. If the Clyde specimens spawn at a similar time this means that the shells of group I are probably one year old. Allowing for an increased growth-rate in the spring and summer the present results agree with this conclusion. Growth continues at a slightly increasing rate until the shell reaches about 34 mm. (the average height of group III), after which there is a marked reduction in the rate (the average height of group IV is 42·1 mm.). This is probably due to the animals reaching maturity which is followed by senescence. A few shells survive to their fourth year and the maximum shell length taken was 47 mm.

No spat of the size reported by Thorsen were found. Unless the spat of *C. septemradiata* can use the mud itself there are very few surfaces for attachment. The shells of group I were all found attached to shells of group III. Such small numbers were found that it is unlikely that the spat depend primarily on older individuals for attachment. It is possible that the spat settle mainly inshore and later migrate to

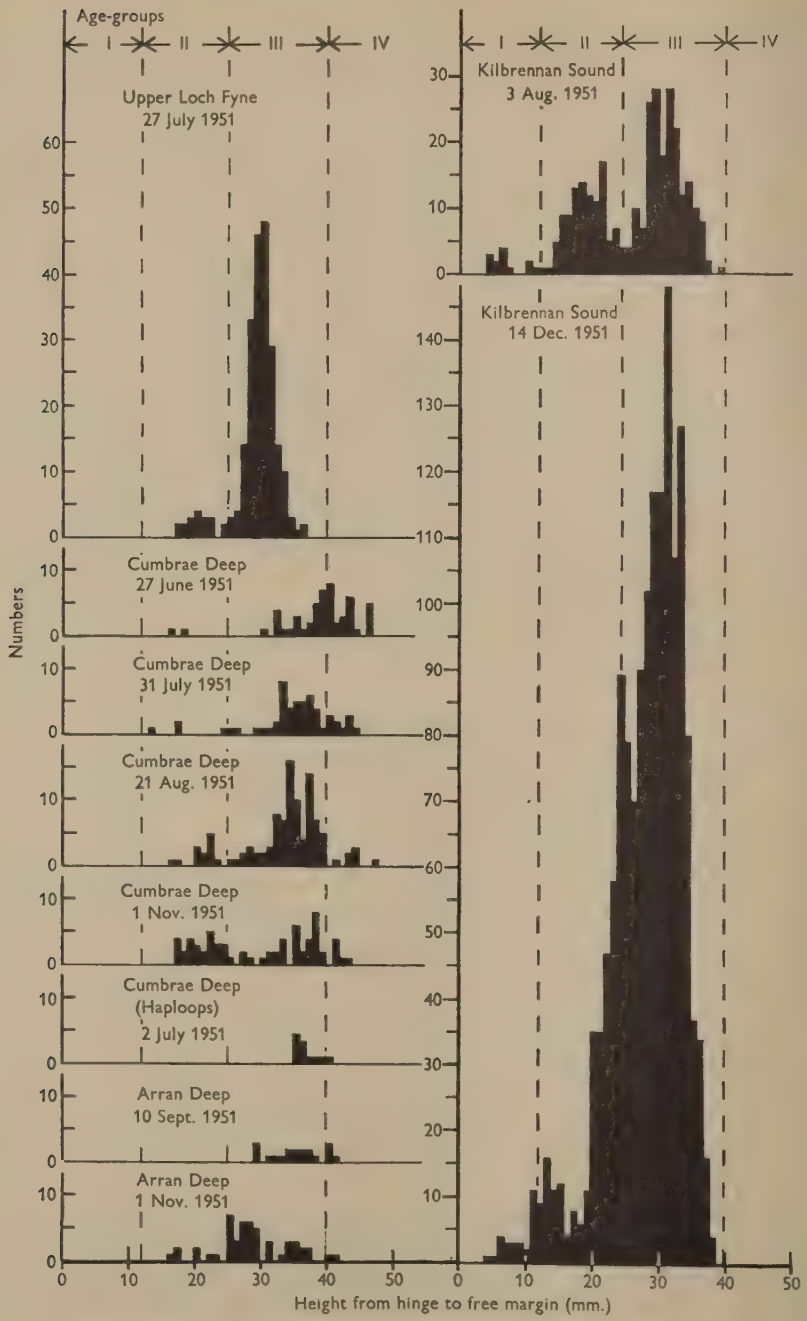

Fig. 4. Height-frequency distribution of the samples of *Chlamys septemradiata*.

deeper water. The spat of *C. opercularis* certainly occur inshore in the Clyde and are found on *Laminaria*, but *Chlamys septemradiata* has not been taken from an inshore habitat. It was found that group II shells in the aquarium will attach themselves by their byssus to the sides of the tank. With group III forming such a large percentage of the population, it is tempting to postulate that the *Chlamys* begin to appear in deep water in their second year and all have completed the migration by the third. However, large numbers in group III may mean that that was a good settlement year.

No marked differences were observed in the shell growth and the composition of the samples between the four localities. The Cumbrae and Arran Deep samples were the only ones that gave group IV shells, while group I only came from the Kilbrennan Sound (Table 3).

Table 3. *Percentages of the total number of shells taken from each locality belonging to each age-group*

Group	Cumbrae Deep	Arran Deep	Kilbrennan Sound	Upper Loch Fyne
I	—	—	1·7	—
II	17·2	10·1	20·2	7·7
III	69·4	86·9	78·1	92·3
IV	13·4	3·0	—	—

Albino specimens were obtained from the Cumbrae Deep (3), Kilbrennan Sound (7) and Upper Loch Fyne (1). These shells belonged to groups II and III. These shells are lying on the same side as the coloured shells. The periostracum appears to be similar, and transverse sections of the mantle edge do not differ from those of the coloured shells. Apart from the lack of brown pigment they appear to be identical with the coloured shells.

EPIFAUNA

The fourteen species listed below were found attached to *C. septemradiata*.

Foraminifera
- *Crithionina heinckei* Rhumbler
- *Rhabdammina cornuta* Brady
- *Planorbulina mediterranensis* d'Orbigny
- *Truncatulina lobulata* (Walker & Jacob)
- *Hyperammina arborescens* (Norman)

Porifera
- *Sycon ciliatum* Fabricius

Annelida
- *Sabella pavonina* Savigny
- *Hydroides norvegica* Gunnerus

Ectoprocta
- *Triticella pedicellata* Alder

Cirripedia
- *Balanus crenatus* Bruguière
- *Verruca stroemia* (Müller)

Lamellibranchia
- *Hiatella arctica* (Linné)
- *Anomia ephippium* Linné

Tunicata
- *Styela coriacea* (Alder & Hancock)

All, with the exception of one specimen of *Hiatella arctica*, were on the uppermost valve of the shell. A record was made of the epifauna on each shell and, with the exception of the Foraminifera, the position on the shell was noted. Measurements of the epifauna were taken where possible (Table 4).

Crithionina heinckei. This was the most frequent animal found on *Chlamys septemradiata* and was found at all the stations sampled. It was first recorded and described by Rhumbler (1928) at Heligoland (Ostmole), and then by Korringa (1951) on *Ostrea*

edulis at Oosterschelde. Both are shallow water localities, and this is the first time that this species has been recorded outside the North Sea and in deep water. It is surprising that it has not been recorded at Millport before, for it is both conspicuous and common. David Robertson never recorded it, and it is not in his collection at the Marine Station.

Nothing new has been found out about this species, details of which are given by Korringa. It occurred on approximately the same numbers of shells in all the localities,

Table 4. *Percentage of shells of* Chlamys septemradiata *affected by epifaunal species*

	Upper Loch Fyne					Kilbrennan Sound				
Age-groups ...	I	II	III	IV	Total	I	II	III	IV	Total
Crithionina heinckei	—	27·3	58·3	—	55·8	25·0	53·7	76·6	—	71·4
Rhabdammina cornuta	—	—	17·2	—	15·6	—	19·7	53·2	—	45·2
Truncatulina lobulata	—	—	—	—	—	—	8·2	15·1	—	13·4
Planorbulina mediterranensis	—	—	—	—	—	—	1·1	15·2	—	11·8
Hyperammina arborescens	—	—	—	—	—	—	—	—	—	—
Sycon ciliatum	—	—	1·0	—	0·9	—	2·9	23·6	—	18·8
Sabella pavonina	—	—	—	—	—	—	—	0·07	—	0·05
Hydroides norvegica	—	—	—	—	—	—	0·3	1·0	—	0·8
Triticella pedicellata	—	—	1·5	—	1·3	—	—	—	—	—
Balanus crenatus	—	—	—	—	—	—	—	0·07	—	0·55
Verruca stroemia	—	—	—	—	—	—	—	0·2	—	0·2
Hiatella arctica	—	—	—	—	—	—	—	0·7	—	0·5
Anomia ephippium	—	—	0·5	—	0·4	—	0·9	3·1	—	2·6
Styela coriacea	—	9·9	14·2	—	13·8	—	0·3	13·7	—	10·6

	Arran Deep					Cumbrae Deep				
Age-groups ...	I	II	III	IV	Total	I	II	III	IV	Total
Crithionina heinckei	—	42·9	59·3	100·0	59·4	—	22·2	67·9	80·0	62·7
Rhabdammina cornuta	—	—	30·5	66·7	28·9	—	4·4	22·8	28·0	20·8
Truncatulina lobulata	—	—	8·5	33·3	8·7	—	—	5·4	2·0	3·9
Planorbulina mediterranensis	—	—	—	—	—	—	—	2·2	—	1·4
Hyperammina arborescens	—	—	6·8	—	5·8	—	—	—	—	—
Sycon ciliatum	—	—	5·1	—	4·3	—	—	0·5	—	0·4
Sabella pavonina	—	—	—	—	—	—	—	1·6	16·0	4·0
Hydroides norvegica	—	—	—	—	—	—	—	10·9	4·0	7·8
Triticella pedicellata	—	—	13·6	33·3	13·0	—	4·4	26·1	50·0	26·9
Balanus crenatus	—	—	—	—	—	—	—	7·1	16·0	7·5
Verruca stroemia	—	—	—	—	—	—	—	—	—	—
Hiatella arctica	—	—	1·7	—	1·5	—	—	—	4·0	0·7
Anomia ephippium	—	—	3·4	66·7	5·8	—	—	7·1	2·0	5·0
Styela coriacea	—	—	47·5	100·0	42·0	—	—	6·5	44·0	12·2

the percentages being: Cumbrae Deep 62·7%, Arran Deep 59·4%, Kilbrennan Sound 71·4%, Upper Loch Fyne 55·8%. As would be expected, at all the stations older shells were most affected, although there is an indication that the percentage of shells with *Crithionina* decreases between June and December (Table 5).

It occurred all over the upper valve of the shell, and on other epifaunal animals such as *Styela*. The diameter of the test is up to 2·5 mm. No record was made of the numbers per shell except that it ranged from 1 to 60, and the number of shells with 20 or more specimens were noted. No group I shell had more than 20 specimens attached, while 2·9% of group II, 38·4% of group III and 46·3% of group IV had more than 20 *Crithionina* on the upper valve. These figures also show the increase in numbers with age.

Rhabdammina cornuta. This is the first time that this species also has been recorded for the Clyde Sea Area, and it was present at all the localities sampled. Of the Foraminifera it was the next most frequent to *Crithionina*. It has been well described by Brady (1884) in the *Challenger* reports. The animal is irregularly branched and the test is made up of fairly coarse sand grains. It showed no preference for any part of the shell, and up to eight specimens of varying size were found on a single shell. It was not present on any of the group I shells, and of the group II shells it was only present on those from the Cumbrae Deep and Kilbrennan Sound. Again there was an increase in the percentage of the shells affected as the shells got older. The sample from the Kilbrennan Sound had the highest number of shells affected—45·2%, with Upper Loch Fyne 15·6%, Arran Deep 28·9% and Cumbrae Deep 20·8%.

Planorbulina mediterranensis. Scott-Elliot, Laurie & Murdoch (1901) list this species as being widely distributed, while Chumley (1918) records it from the Arran Basin and Upper Loch Fyne. It was only found on *Chlamys septemradiata* taken from the Kilbrennan Sound and Cumbrae Deep. *Planorbulina* from the Kilbrennan Sound

Table 5. *Percentages of shells of* Chlamys septemradiata *affected by* Crithionina *in the different age-groups*

		Age-groups				
		I	II	III	IV	Total
Kilbrennan Sound	August	8·1	79·6	93·8	—	82·9
	December	35·3	46·4	73·9	—	66·7
Arran Deep	October	—	42·9	63·5	100·0	61·0
	November	—	—	50·0	100·0	52·6
Cumbrae Deep	June	—	100·0	56·0	83·3	70·5
	July*	—	—	80·0	100·0	81·9
	July	—	33·3	75·0	79·0	72·2
	August	—	23·1	60·0	42·9	54·0
	November	—	14·8	59·2	100·0	41·5
Upper Loch Fyne	July	—	27·3	58·3	—	55·8

* Taken from the *Haploops* association.

samples was found on 1·1% of the total number of group II shells and on 15·2% of group II. It was found only on group III shells from the Cumbrae Deep and in two of the samples only (July and November), the July sample was taken from the *Haploops* community. Shells with *Planorbulina* form 1·4% of the total catch from the Cumbrae Deep. There were never more than three specimens on a shell, and they were not restricted to any particular region of the shell. The majority of the specimens were approximately 2·0 mm. in diameter.

Truncatulina lobulata. This species is also recorded by Scott-Elliot *et al.* (1901) as being common throughout the area. Chumley reports it from the Arran Basin and Upper Loch Fyne. In the samples of *Chlamys septemradiata* it was present from all localities except Upper Loch Fyne. There were up to 20 specimens on each shell and the total numbers of shells affected at each locality were as follows: Kilbrennan Sound 13·4%, Arran Deep 8·7% and the Cumbrae Deep 3·9%. They were not restricted to any particular region of the shell and were present on groups III and IV shells. Only in the samples from the Kilbrennan Sound was *Truncatulina* present on group II shells—on 8·2% of the total number of shells of this group in the sample.

Hyperammina arborescens. Scott-Elliot *et al.* state that this species is abundant and generally distributed between 20 and 60 fathoms, frequently on annelid tubes. Chumley also records it from all stations, but in the present sampling it was only found on shells from the Arran Deep. It was only present on group III shells with a maximum of six specimens on each shell; the affected shells represented 5·8% of the total catch.

Sycon ciliatum. In 1901 *Sycon ciliatum* was reported as being common throughout the Clyde Sea Area, but Chumley only recorded it from Loch Goil and the Dunoon Basin, and in both localities as being rare. It was taken from all localities but only in the Kilbrennan Sound in large numbers (see Table 4). In the Upper Loch Fyne and Cumbrae Deep samples it was present on two and one specimens of *C. septemradiata* respectively, and only three from the smaller Arran Deep samples. The Cumbrae Deep specimen was from the *Haploops* community. All the above specimens were on group III shells. On the Kilbrennan Sound samples it was recorded from groups II and III shells forming 2·9 and 23·6% respectively of the total number of shells from these groups. Some shells had more than one specimen attached, and the maximum number recorded was five. The percentages of shells with *Sycon* were: 71·2% with one specimen, 21·6% with two, 5·2% with three, 1·7% with four and 0·3% with five. The total number of *Sycon* taken was 446. Fig. 5 shows the numbers of the large December sample (see below) plotted against length, and there is some indication that there may be two populations. Orton (1914) found that *Sycon* on the shore at Plymouth were annuals, but that they had two breeding seasons, one in late May and early June and one in October. The Kilbrennan Sound samples were taken in August and December, only 13 shells in the former sample had *Sycon* (7·4%) all on group III *Chlamys*. The December sample contained 304 *Sycon* on group III shells; 26·1% of the group III shells were affected; 55·4% of the sponges were 4 mm. and less in length. This suggests an autumn settlement. The existence of two populations is supported by the examination of the position of the *Sycon* on the shell. The positions for *Sycon* on all group III shells of the December sample were plotted on a single shell. Those sponges, 6 mm. or over in length, were assumed to be an older population and plotted separately (Fig. 6*b*). It will be seen that almost all of those that are 6 mm. and above lie within the area of the average size for group II shells. The two specimens close to the free margin were 6·5 and 7·4 mm. long respectively, and thus probably belong to the younger population. The area outside the broken line will therefore represent the growth from June to December. This also supports the view that the age groups of *Chlamys septemradiata* are in fact year groups. Fig. 6 also shows that there is an apparent preference for the hinge area. Day & Wilson (1934), and many other workers, have shown that the young stages of marine invertebrates can select

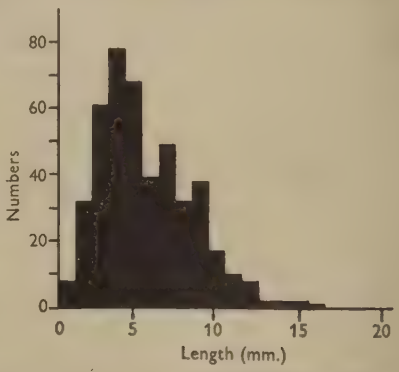

Fig. 5. Length-frequency distribution of *Sycon* taken from group III shells of the sample from the Kilbrennan Sound (14 December 1951).

the substratum on which they will settle. However, in the case of *Sycon* it is not necessarily a searching reaction. It has been pointed out (p. 243) that *Chlamys septemradiata* is an active animal, and it may be that when young *Sycon* attempt to settle on the shell the ones near the free margin tend to be thrown off, while those at the hinge region are able to attach themselves.

It must be noted that the maximum size attained by the Clyde specimens is considerably less than those from the shore at Plymouth measured by Orton. The maximum size he recorded was 24·8 cm. while the maximum size recorded from the present samples is 1·6 cm. The main settlement is obviously on group III shells. This supports the theory that there is a migration to the deeper water at the end of the second year. There are no group (2) *Sycon* on the few second-year shells that are present, and this possibly indicates that these have arrived at the deeper water in the late summer.

Fig. 6. Positions of *Sycon* for the sample taken from the Kilbrennan Sound (14 December 1951) plotted on a single shell. (*a*) group (1) *Sycon* on group III *Chlamys*. (*b*) group (2) *Sycon* on group III *Chlamys*. The chain-dotted line represents the free margin of a group II *Chlamys*. The area below the broken line represents the growth from June to December. (*c*) group (1) *Sycon* on group III *Chlamys*.

Sabella pavonina. Scott-Elliot *et al.* (1901) and Chumley (1918) record *Sabella* as being common throughout the area. With the exception of one specimen on a group III shell from the Kilbrenan Sound, the only specimens of *Sabella* on *Chlamys* came from the Cumbrae Deep. These were present in all the samples except that from the *Haploops* community, and they were only present on shells of groups III and IV; 1·6% of group III and 16·0% of group IV shells had *Sabella* attached. Apart from two shells with one specimen there were always three to six specimens per shell, while three had 14, 15 and 17 specimens respectively. In addition, all but three of the shells had *Styela coriacea* attached. There appears to be a marked tendency for the *Sabella* to be attached to the test of the tunicate rather than the shell itself. Thus 68 specimens of a total of 79 were attached to the tests of *Styela*, all to the largest specimens—1·8 cm. and above, i.e. the older population (see p. 256). It would appear that there is a selection of the substratum as shown by Day & Wilson (1934) and other workers for many other polychaetes. The Cumbrae Deep samples have by far the largest

number of *Styela*, probably because of the high percentage of group IV shells present. On group III shells the maximum tube length was 1·5 cm. and on group IV shells 6·5 cm. There is apparently only one age-group present (Fig. 7) with 76% of the present samples being 2 cm. or less. Since Orton (1914) found that *Sabella* secreted a tube 12·6 cm. long in less than 31 weeks, it is probable that the majority of the *Sabella* taken are about six weeks old. Allen (1915) states that breeding takes place in August and September in Plymouth. It is probable that the Clyde specimens are breeding from the beginning of June to September. Unless they are able to continue their growth on the bottom after the death of the *Styela*, the greater part of the *Sabella* must live one year or less, and must be recruited afresh every year.

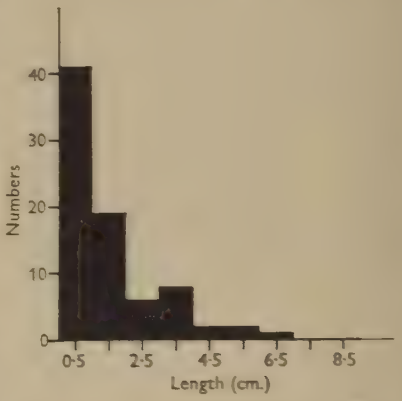

Fig. 7. Numbers and lengths of *Sabella*.

Hydroides norvegica. Scott-Elliot *et al.* (1901) list *Hydroides* as occurring only in 10–15 fathoms off Cumbrae, while Chumley does not list it. In the sublittoral survey of the area from 1949 onwards it has been recorded as being common on rocky and coarse shell gravel bottoms. It was found on the shells from the Kilbrennan Sound and the Cumbrae Deep. Less than 1% of the Kilbrennan Sound sample had *Hydroides* present and these were found on groups II and III shells. There is an overall percentage of 7·9% (group III 10·9%, group IV 4·0%) from the Cumbrae Deep. There were never more than two specimens on a shell, and owing to the variation in shape of the tubes no measurements were taken. *Hydroides* was found to coil both sinistrally and dextrally.

Triticella pedicellata. This species is not recorded by Scott-Elliot *et al.* and is only recorded from Loch Goil in 45 fathoms by Chumley. It was present on shells from all the localities except the Kilbrennan Sound. In the Upper Loch Fyne samples it was present on 1·5% of the group III shells. It was more common on the Arran Deep and Cumbrae Deep shells, being on 13·0 and 26·9% of the total number of shells respectively. *Triticella* was present on shells of groups III and IV from both of these localities, and on group II shells of the Cumbrae Deep samples. It was sometimes present in very large numbers and there is a tendency to concentrate at the periphery of the shell.

Balanus crenatus is common throughout the area, and much detailed work has been carried out on this species in the Clyde (Pyefinch 1948; Barnes & Bagenal 1951; Barnes, Crisp & Powell 1951, and others). There were very few *Chlamys* with *Balanus* attached, but Barnes & Bagenal report that in the older age-groups of *Nephrops*, which is caught on the same grounds as *Chlamys septemradiata*, a high percentage of their samples (often 100%) had *Balanus* attached. These workers were able to correlate the lack of barnacles on the younger *Nephrops* with the fact that the latter can build a burrow that will cover them completely.

With the exception of one specimen from the Kilbrennan Sound all were taken from the Cumbrae Deep. These were attached to 7·5% of the total number of shells taken and were only found on shells of groups III and IV. A maximum number of three *Balanus* per shell was recorded and the largest size was 1·9 cm. Although only 26 specimens were taken they can be divided into two groups (Fig. 8). The larger size-group, which is present in the summer samples, is almost certainly the spring spat of 1950, and the smaller size-group the spatfall of autumn 1950, while specimens of 2 mm. and less will probably be the spring spat of 1951.

Verruca stroemia. This species is recorded in the 1901 list as frequent on shells and stones throughout the Clyde. In the present samples it was recorded from the Kilbrennan Sound only in both the December and the August sample. Only four specimens were taken and these were very small (2·0, 1·3, 4·2 and 2·2 mm.). These represent less than 0·3% of the total number of shells taken.

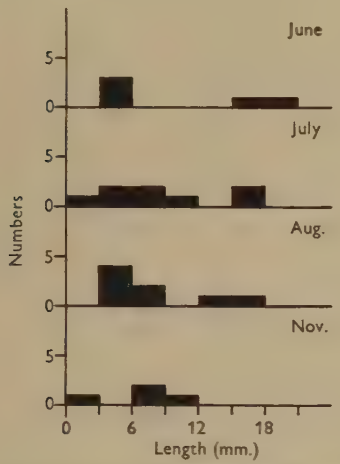

Fig. 8. Numbers of *Balanus* plotted against length in four samples.

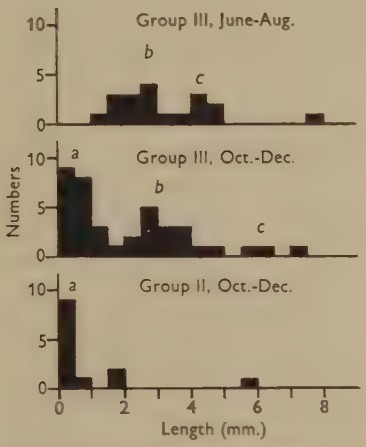

Fig. 9. Numbers and lengths of *Anomia*. *a*, *b* and *c* indicate three age-groups.

Anomia ephippium is common throughout the area. It was found in small numbers on shells from the four localities and in all the samples, except the first taken from the Cumbrae Deep and from the Kilbrennan Sound (May and August respectively). The small sample from the *Haploops* community was interesting in that seven of the eleven shells taken had *Anomia* attached. Two shells had one, and the others 2, 5, 8, 8, 9 specimens respectively. Ninety-two *Anomia* were taken and the maximum shell-height (umbo to free margin) was 7·9 mm. The numbers were sufficient to give some indication of age-groups and time of settlement (see Fig. 9). The measurements of *Anomia* taken between June and August were grouped together as were those taken between October and December. No group II shells were taken with *Anomia* attached in the former months. Three size groups were found. (*a*) New spat settling between October and December on groups II, III and IV shells. The majority of these were taken from the large December sample from the Kilbrennan Sound. The size of the

spat ranged from 0·5 to 1·5 mm. Apart from one specimen, measuring 5·5 mm., and one measuring 2·0 mm. (the latter probably belonging to this size-group) all *Anomia* on group II shells belonged to this group. (*b*) This group ranged from 2·0 to 3·5 mm. (average 2·5 mm.) in height in the samples taken from June to August and from 2·5

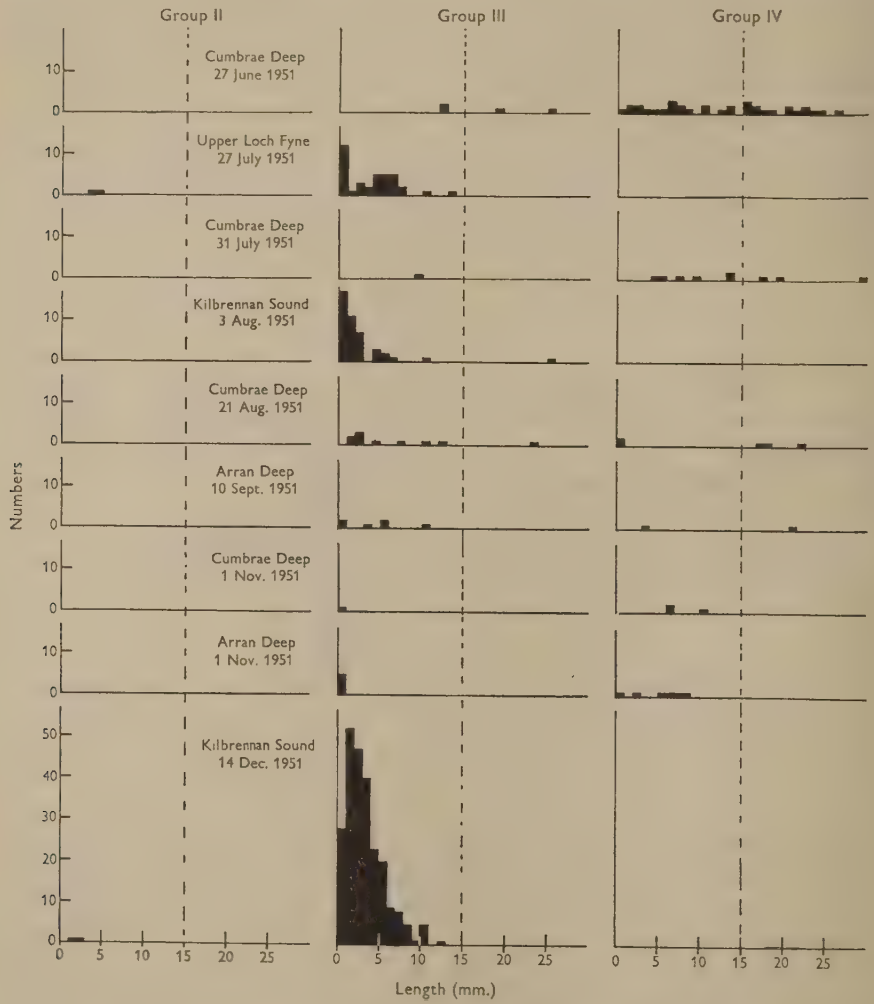

Fig. 10. Numbers and lengths of *Styela* on groups II, III and IV shells from all the samples taken.

to 4·5 mm. (average 3·5 mm.) in the samples from October to December. As the former figures were taken mainly from the July sample from the Cumbrae Deep and the latter from the December sample, these figures show the growth over this period. This group was only taken on group III shells. (*c*) There is also a small size-group between 4·0 and 5·0 mm. in the June to August samples, and it is probable that this

group is represented by the few shells measuring 6·0–6·5 mm. in the October to December samples.

Hiatella arctica. This species has been recently studied by Hunter (1949) who worked on specimens from the Clyde. It was found in three samples: the December sample from the Kilbrennan Sound, the November sample from the Arran Deep, and the June sample from the Cumbrae Deep. Very few specimens were taken; 0·5% of the total number of *Chlamys septemradiata* from the Kilbrennan Sound were affected, 1·5% of the Arran Deep shells and 0·7% of the Cumbrae Deep shells. The size ranged from 1·0 to 16·0 mm., and up to four specimens were found on each shell. They were only taken from shells of groups III and IV.

Styela coriacea. This species is not listed by Scott-Elliot *et al.* (1901) nor is it recorded by Chumley (1918), although *Styela rustica* (L.)* is recorded as being common. The recent survey has shown that *S. coriacea* is fairly common within the Clyde Sea Area. It is found mainly on *Chlamys septemradiata* and occasionally on other shells. It was found at the four localities sampled. Shells from the Arran Deep were most affected with 42·0%, Kilbrennan Sound had 10·6%, Cumbrae Deep 12·2% and Upper Loch Fyne 13·8%. Only four group II shells were taken with *Styela*, two from Upper Loch Fyne and two from the Kilbrennan Sound and all were small specimens not more than 5 mm. long. The longest basal measurement was taken. *Styela* was present on group III shells from all samples. Population histograms show (Fig. 10) that 86·1% of the specimens taken were 1·0 cm. or less, and that 50·0% were less than 0·3 cm. They also indicate that breeding is probably continuous throughout the year. There were some *Styela* that were over 1·5 cm. in length, and it is likely that these are the remnants of the population of the previous year. Consideration of group IV shells shows that the larger *Styela* disappear from the samples by the beginning of October. Thus *Styela* mainly occurs upon shells of groups III and IV, absence on group II shells again suggests that there is a migration of *Chlamys* to the deeper water at the end of the second year.

Styela resembles *Sycon* in that both settle mainly in the hinge area, see Fig. 11. The reasons why they should settle in this area have been discussed (p. 253). The area of the attaching base is often so great that only one specimen can settle in the hinge region, and in all but three cases where there is more than one *Styela* on the shell it is the largest that is at the hinge. Of the 281 shells with *Styela* attached 36 have two, 10 have three, 6 have four and 4 have five specimens on each shell.

THE EFFECT OF THE EPIFAUNA ON *CHLAMYS SEPTEMRADIATA*

The epifauna might be expected to affect *Chlamys septemradiata* in two ways; the weight of the epifauna may hamper swimming, and epifauna settling on the hinge of the shell may affect the efficiency of the ligament with similar results. However, the only animal that was seen to cover the hinge was one specimen of *Styela* which had apparently no effect on the hinge movement. The number of epifaunal animals,

* Berrill (1950) does not include *S. rustica* as a British species in *The Tunicata*. *S. rustica* is recorded as being common in the Clyde Sea Area both in the 1901 list and in Chumley (both are taken from the 'Medusa' records (1884–92) of Sir John Murray), neither lists *S. coriacea*. In the recent Clyde Survey only *S. coriacea* has been found and it would appear that the lists of 1901 and Chumley should read *S. coriacea* and not *S. rustica*.

their position on the shell and their combined weight are the primary factors. The maximum number of animals on the shell varies from 60 in the case of Foraminifera to not more than five in the case of the larger animals. Often there is more than one species on each shell, but it is the larger animals that will be the most important. These are *Styela*, *Sabella*, *Anomia* and *Balanus*. The maximum individual dry weights recorded were *Styela* 0·08 g., *Sabella* 0·15 g., *Anomia* 0·05 g. and *Balanus* 0·16 g. The maximum recorded dry weight of epifauna was 0·73 g. This is 27·5% of the average dry weight of a group III *Chlamys* (2·65 g.). Only five *C. septemradiata* were taken that had attached epifauna with a dry weight of this order.

Styela and *Sabella* are the two epifaunal animals whose growth-rate is the most rapid, and are the ones that might be expected to be harmful. *Styela* is an annual and it is only in the last six months of its life that it will be large enough to have any effect. As the occurrence of *Sabella* is correlated with that of *Styela* it is only when *Styela*

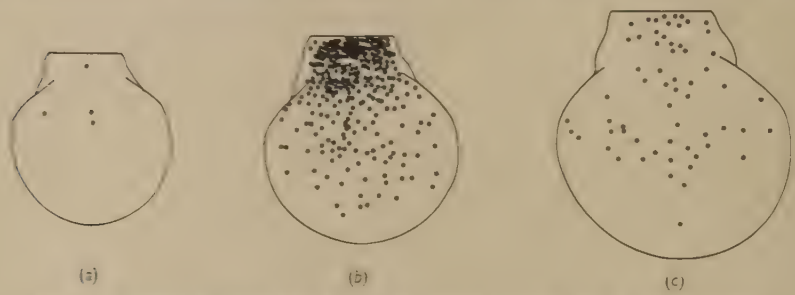

Fig. 11. Positions of *Styela* from all samples plotted on single shells. (*a*) distribution on group II shells; (*b*) on group III shells; (*c*) on group IV shells.

has become established that *Sabella* could have any effect, and before *Sabella* is large enough the tunicate will have died. The other large epifaunal species, particularly those that live for more than one year, grow relatively slowly and therefore will not grow to any great size during the life of *Chlamys septemradiata*.

Most members of the epifauna do not become established before the end of the second year of the life of *C. septemradiata*, so that it is only during the last year or year and a half of its life that the bivalve is likely to be affected.

POPULATIONS OF *CHLAMYS SEPTEMRADIATA*

These results indicate that there are probably distinct populations of *Chlamys* within the Clyde Sea Area. The epifauna animals on *C. septemradiata* (see Table 4) are different in the four localities, although previous sampling has shown that these animals are evenly distributed farther inshore throughout the area. Shells from Cumbrae Deep are characterized by the presence of *Sabella pavonina*, *Hydroides norvegica* and *Balanus crenatus*, these animals occurring infrequently at the other localities. *Triticella pedicellata* occurs on over a quarter of the specimens taken, and represents the highest percentage of the four localities. Of the other localities only the Arran Deep has any numbers of this animal present. The small sample from the *Haploops* community has a very high percentage of epifauna, particularly *Anomia*

ephippium and *Hydroides norvegica*. The infauna at this station is also very rich and the bottom is approaching a muddy gravel.

Arran Deep is characterized by having the highest percentage of *Styela*, and it is the only locality from which *Hyperammina* was taken, although records show that this species is common throughout the Clyde. The shells from this locality have the highest percentage of *Hiatella*, although this species is not common on *Chlamys septemradiata*. Kilbrennan Sound has the highest percentage of Foraminifera present and, apart from a few specimens in the Cumbrae Deep, all the *Sycon* that were taken. It also had the only specimens of *Verruca stroemia* that were taken. Apart from *Triticella* and *Hyperammina* all other species of epifaunal animals were present in small numbers. Upper Loch Fyne was characteristic in its lack of epifaunal species, only six species being recorded, none of them characteristic of the locality. As in the other localities, *Crithionina* and *Rhabdammina* were present in large numbers.

It has been shown that in *Chlamys septemradiata* there is variation with respect to the rib numbers and the depth of the ribs, those from the Cumbrae and Arran Deeps being different from those taken from the Kilbrennan Sound and Upper Loch Fyne. Samples from the last area may be expected to differ from the rest because of the shallow barriers at the Minnard Narrows and the Otter Spit separating this area from the Arran Deep. But there is no geographical reason why the others should not intermingle. The Arran Deep and Kilbrennan Sound localities are only seven miles apart. It would appear that although *C. septemradiata* can swim and possibly migrate it does so within the limits of these localities.

ACKNOWLEDGEMENTS

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SUMMARY

1. A study has been made of the epifauna of deep-water muds with special reference to *Chlamys septemradiata*. Details of the biology of *C. septemradiata* and information on growth-rates and length of life of some of the attached animals has been obtained. The samples were taken from four localities of the Clyde Sea Area—Cumbrae Deep, Arran Deep, Kilbrennan Sound and Upper Loch Fyne.

2. *C. septemradiata* lives for three and a half years. Two distinct populations have been found, one with five-, six- and seven-ribbed shells, each representing about 30% of the population, and deep undulating ribs, the other with shallow undulating ribs in which shells with seven ribs represent 50% of the population, while those with five ribs form 8% of the population. No colour differences were noted between the different localities but albino specimens were obtained comprising 0·4% of the total number of shells examined.

3. Third-year shells are the most common. All the first-year shells were taken attached to third-year shells. Second-year shells also were found to attach themselves to the sides of the aquarium. Evidence shows that the spat probably settle inshore and migrate to deep water at the end of the second year.

4. Fourteen epifaunal species were obtained from the upper valves of *C. septemradiata*. Details of the percentage infection, length of life, growth-rate and settlement are given.

5. *Sycon* and *Styela* were found to have a preference for the hinge area of the shell. Other epifaunal species do not appear to settle in any particular region of the shell.

6. The epifauna has no harmful effect on *C. septemradiata*.

7. The epifaunas at the different localities are compared.

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AN ECOLOGICAL STUDY OF THE FEEDING HABITS OF THE ENGLISH TITMICE

By P. H. T. HARTLEY, M.A.
Edward Grey Institute, Department of Zoological Field Studies, University of Oxford

(With 16 Figures in the Text)

INTRODUCTION

Problems of the interaction between predatory animals and the species whereon they feed may be attacked in two ways. When the predator species is sufficiently numerous and the prey is amenable to accurate sampling the advance may be direct. But when the predator is scarce or its foods are diverse; when the prey species are so inaccessibly or unevenly dispersed that they cannot be quantitatively surveyed, then indirect methods of investigation must be used.

Early in 1947, at the request of the Agricultural Research Council, the Edward Grey Institute of Field Ornithology began an investigation of the dual problem of the influence of bird predation upon the numbers of the prey species and of the influence of the stocks of prey upon the population level of the carnivores. It was agreed that species of economic importance should not be studied, so that the work should not be done upon birds directly dependent on man's activities for a major part of their food supply. The species selected for study must be resident throughout the year, and must be abundant. Here a difficulty was found, for few bird species, even those usually described as 'common' or 'abundant' are represented in any habitat in such numbers that adequate sampling will not sensibly modify, or even destroy the stock in the course of the investigation. This difficulty in choice of species suitable for a direct approach was especially marked after the decimation of the stocks of so many passerine birds in the great frost of early 1947 (Ticehurst & Hartley 1948). It was therefore decided to make an indirect attack upon the problem by the application of a principle enunciated by Charles Darwin (1859): 'As the species of the same genus usually have, though by no means invariably, much similarity in habits and constitution, and always in structure, the struggle will generally be more severe between them, if they come into competition with each other, than between the species of distinct genera.'

A group of closely related species, all reasonably abundant, was needed for work on the implication of this principle. In the English Midlands the Paridae (titmice) were an obvious choice. Four species were to be found regularly feeding in the same habitats: great tit, *Parus major* L.; blue tit, *P. caeruleus* L.; coal tit, *P. ater* L.; marsh tit, *P. palustris* L. Certain ecological conclusions could be drawn from the results of study of the feeding habits of four congeneric species living side by side. If no distinctions could be made between the foods, feeding places and feeding methods of the four species it might reasonably be assumed that food supply was not the factor limiting their numbers. Conversely, a measure of ecological separation between the species would justify the assumption of some degree of interspecific pressure. Lack

(1944), summarizing the almost invariable occurrence of ecological differences between closely allied species of passerine birds in the British Isles, remarked on the scanty knowledge of distinctions between the titmice and wrote: 'Hence in the British forms of *Parus* there is wide overlap in habitat, but detailed study of food and feeding habits might perhaps show a greater degree of ecological separation than this summary suggests.'

Studies of stomach contents alone, without data on sources of supply cannot solve the problems of interspecific feeding relationships with finality, even if adequate sampling be possible. The discovery of the same food organisms in all the species examined does not prove interspecific competition, unless it be also proven that all the predator species have investigated all the sources of supply with equal diligence and that the stock of food is inadequate for their needs. The finding of different foods in different species is not irrefutable proof of the absence of competition, unless it be shown that all selection of foods is by choice and choice alone from diverse super-abundant food stocks, all equally accessible to all the species studied.

After some preliminary trials of methods, the feeding habits of the four species of titmice already listed and those of two other birds—the willow tit, *P. atricapillus* Hellm. and the long-tailed tit, *Aegithalos caudatus* (L.)—were studied over a period of two and a half years, from the early summer of 1947 to the end of January 1950. A record was made for each feeding bird of the height from the ground at which it was at work, the species of tree or bush wherein it was and of the feeding 'site'. In trees and shrubs the 'sites' were classified into: trunk; limb—any main member more than 1 ft. in diameter; branch—any member between 1 ft. and 2 in. in diameter; twig—less than 2 in. in diameter; leaves, flowers, buds, fruits, etc. The heights of the feeding activities were sometimes measured with a simple level; sometimes ascertained by comparison with objects of known height; and sometimes estimated. A check of estimates against measured heights showed that they gave the accuracy needed—$\pm$ 5 ft.

An arbitrary rule was adopted of 'One tree—one record'. So long as a titmouse continued in one tree, only one record was made, that of the height whereat the bird first alighted or was first seen. Titmice have no set method of working a tree, comparable with the steady ascent of the treecreeper, *Certhia familiaris* L., so that the 'height when first seen' rule does not weight the records in favour of the lower levels. The 'one tree—one record' rule has the disadvantage of emphasizing small shrubs of one species visited in rapid succession as compared with the large tree wherein hunting may be prolonged. But the alternative, timing by stop-watch the period spent in each tree, would be impossible in high summer, when a feeding bird may be glimpsed for a few seconds after minutes of scrutiny of the foliage. Timing would also reduce the number of records which could be made from a flock, since attention would be confined to a single bird. This would be a disadvantage in the post-breeding season; then a couple of empty hours may be followed by a few crowded minutes when a tit flock is at last encountered.

This study was made within an area in south Oxfordshire and north Berkshire. The boundary runs from Eynsham south-south-east to Abingdon east-south-east to Wallingford and thence north-west to Oxford and so to Eynsham, enclosing a wedge of country some 15 miles long and 5 miles wide at the base. In the north-west corner

of the area is the Wytham estate, owned by the University of Oxford, containing two woods. Wytham Great Wood, the scene of the most intensive study of the feeding titmice, stands on a bluff of Jurassic clay, capped with coralline crag, fronting the Midland Plain. It is a mixed deciduous wood; the predominant trees of the canopy are oak, *Quercus robur* L., sycamore, *Acer pseudo-platanus* L., and ash, *Fraxinus excelsior* L., with sallow, *Salix caprea* L., hawthorn, *Crataegus oxyacantha* L., black thorn, *Prunus spinosa* L., hazel, *Corylus avellana* L. and elder, *Sambucus nigra* L., in the shrub layer, and bracken, *Pteridium aquilinum* (L.) Kuhn, and brambles, *Rubus* sp. in the undergrowth. There are two plantations of spruce, *Picea abies* (L.) Karsten, larch, *Larix* sp., and Douglas fir, *Pseudotsuga taxifolia* (Poir.) Britt., and a few clumps of spruce and Scots pine, *Pinus sylvestris* L. Marley Wood, the smaller wood of the estate, where some observations were made, stands on clay, and has more hazel and birch, *Betula* sp., and fewer conifers.

Near the southward tip of the area is the village of Brightwell-cum-Sotwell, a second scene of close study. The long, narrow village stands north of the Berkshire Downs, and has large orchards, many walnut trees, *Juglans regia* L., and big hedgerow elms, *Ulmus* spp. Many records were made in north Oxford, where there are large gardens and big trees, including beech, *Fagus sylvatica* L., and horse chestnuts, *Aesculus hippocastanum* L., and variety of ornamental shrubs. Observations were made at many other places in the well-timbered agricultural country between Oxford and Wallingford.

A concentration upon the birds of a single habitat would give results certainly partial and probably misleading. The distribution of the titmice varied greatly with the seasons. Many woodland-bred birds wandered in late summer to the hedgerows of the farmed land. In winter the titmouse populations of village and town gardens were notably bigger than in the breeding season. This is illustrated by the seasonal variations in the number of records from Brightwell and from north Oxford, where occasions of observation were, by and large, equal from month to month. Birds ringed at Wytham have been recovered in north Oxford, and a great tit ringed in Wytham Great Wood traversed the whole area, being recovered in Brightwell two years later (Gibb 1950). To the study the titmice of one habitat would be to study only a part of the natural history of the species.

A word may be said about the extremely simple statistical treatment of the results. This never goes beyond the demonstration of significance in differences between the numbers of birds feeding at certain levels. The reasons for the simplicity of treatment are three.

(1) The sampling was very far from uniform. The uneven and frequently changing distribution of the titmice defeated any neat scheme of patrols of defined duration, timing and direction. The path which one day led to a gathering of feeding titmice might, within a week, lead directly away from it. The birds had to be sought where their wanderings led, or where temporary abundances of supply had assembled them.

(2) The titmice were not equally visible in all their feeding stations. A blue tit at 60 ft. in a bare oak was more easily seen than a coal tit in a nearby conifer or a great tit feeding among fallen leaves and brambles. It is fortunate that this hindrance of observation tended to minimize differences of distribution, since any ecological

distinctions between the species which emerge are proven in the face of a difficulty of technique tending to mask their appearance.

(3) The distribution of feeding niches was not itself 'normal' about any one level. In an acre of wood the whole of the woodland floor (saving the space taken by the actual boles of trees) was available to feeding birds. At 1 ft. the number of places to stand was reduced, and at each succeeding level the area of surface where titmice might cling and search varied not only with the species of trees and shrubs but also with their mode of growth and the closeness of the stand.

The statement that a difference is 'significant' implies a probability of 0·01 or less. Probabilities between 0·01 and 0·05 are stated.

Owing to lack of space it has been impossible to print the full results of this investigation here, but a copy has been placed in the library of the Edward Grey Institute. Duplicated sets of tables showing the height-frequency distributions of feeding activities have been prepared; copies may be obtained from the Secretary, Edward Grey Institute, Department of Zoological Field Studies, Oxford.

THE HEIGHT DISTRIBUTION OF FEEDING ACTIVITIES

(*a*) *The great tit*

Observations began during the intense frost of February 1947. The ground was snow-covered for most of the month. Great tits hunted chiefly at heights of less than 20 ft.—75 records of 90, including nine instances of feeding on the ground. In March the great tits fed more on the ground than at any other level (25% of 228 records) and there was a slight increase in activity at heights of over 20 ft. There was some evidence that the amount of ground feeding would have been greater had there been less snow (Fig. 1). In 51 records from six days with complete snow cover only one bird was at work on the ground; but in the two days before and the three days after the snow 49 of 112 observations of great tits were of ground feeding. In April feeding activity was fairly evenly distributed up to a height of 24 ft.; there were as many birds feeding on the ground as at any other level.

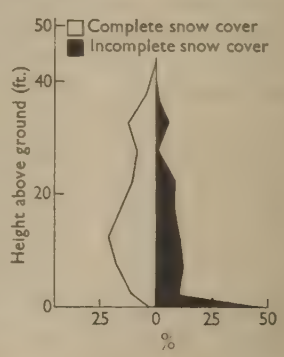


Fig. 1. The effect of complete snow cover on the height-frequency distribution of the feeding stations of great tits, March 1947. In this and the following figures birds feeding clear of the ground but below 5 ft. are grouped at 2½ ft., birds at 5–9 ft. at 7½ ft., and so upward.

In May 1947 there was a marked change in the height distribution of feeding great tits. The modal feeding level was now 15–19 ft., and 45% of the records were of birds at a height of over 20 ft. In this month caterpillars—chiefly the larvae of *Operophtera brumata* (L.) and *Hybernia* spp.—were abundant in the woods, in densities up to 37 per 100 oak leaves. In June, the abundance of caterpillars being ended by the 12th of the month, the higher levels were abandoned. In June, July and August feeding great tits were fairly evenly distributed between the lowest undergrowth and about 20 ft. But few birds fed on the ground.

In September 1947, when 25 of 116 records were of ground feeding, there were significant differences between the great tits of north Oxford on the one hand (37% of

74 records being of birds on the ground) and, on the other, Wytham Great Wood with no birds at work at ground-level and Brightwell with one record of ground foraging out of 27. The Great Wood and Brightwell had many elders in fruit and great tits feeding therein; but this food was not available in the Oxford gardens. In October north Oxford still differed from Wytham Great Wood and Brightwell in the significantly larger proportion of activity on the ground. The Wytham great tits fed much on aphids from the leaves of sycamore and oak, a food abundant in the autumn of this year (Table 1). In November 1947 there was much feeding on the ground in Oxford and Brightwell, but very little in Wytham Great Wood, where aphids were still abundant in the earlier part of the month. This general distribution of feeding birds continued until the end of the year.

1948 opened with the ground as the most frequented feeding place of great tits—35% of the records in January and 37% in February. In Wytham Great Wood 45 and 41% of the observations were of birds on the ground as against only 3 and 2% in November and December 1947. In March the proportion of ground foraging was 26% in the Great Wood, 22% in Brightwell and 34% in Oxford. In Wytham Great Wood the proportion of birds at or above 30 ft. showed a significant increase over that in the previous month. In April 1948 the feeding levels suddenly rose. In Wytham Great Wood the ground was deserted, 20–24 ft. was the modal height and 54% of all foraging was at heights above 19 ft. This sudden change in the habits of the feeding

Table 1. *Numbers of aphids on the leaves of sycamores in Wytham Great Wood*

	No. of leaves	No. of aphids	Aphids per leaf
23–28 Oct. 1947	82	538	6·55
6 Nov. 1947	49	195	3·97
1–15 Oct. 1948	114	32	0·28
7 Oct. 1949	7	58	8·26
3 Nov. 1949	90	185	2·06

great tits coincided with the spring outbreak of defoliating caterpillars, which began nearly a month earlier than in 1947. In May the foraging level most often recorded had dropped a little, but 53% of records were still at or above 20 ft. In June the percentage of activity above 19 ft. had dropped to 43%—the difference is not statistically significant. In July the modal height was 25–29 ft., and the percentage of records of birds foraging above 19 ft. had risen to 57%. (The increase over the proportion in June is not significant.) While the great tits of Wytham were feeding in the trees the few birds which were observed in Oxford in high summer continued to feed much upon the ground. In the four months April to July, 18 of 43 records from north Oxford were of birds foraging on the ground as compared with 12 of 492 records from the Great Wood.

In August 1948 ground hunting was seen in 14 out of the 54 observations in Wytham Great Wood, in statistically significant contrast to July. Only 22% of the records were of birds feeding at 20 ft. or more. In this month a number of great tits were seen feeding in big umbellifers growing beside country roads. In September, 17 of 64 records were of foraging on the ground.

In October 1948 the great tits in the Wytham woods were very differently employed from those at Brightwell. In this year of abundant beech-mast and few aphids

(Table 1) the birds in the Great Wood fed more in beeches than in the previous year (19% of records as against nil in 1947) and less in sycamores and oaks (16·5 and 1·5% of records as compared with 47·5 and 22% in 1947). Only 6 of 106 records are of birds on the ground. In Marley Wood all the observations were of birds in trees bearing nuts or fruit (beech, hazel, elder, hawthorn) and there was no ground feeding. But at Brightwell, where the bulk of a large walnut crop had fallen, 39 of 99 records were of great tits at work on the ground. In November the beech-mast crop had fallen. In Wytham Great Wood, with its few beeches there was little ground feeding, and 56% of the records were very evenly distributed between 10 and 50 ft. At Brightwell also most of the great tits were feeding above ground-level, the proportion of records of ground feeding differing significantly from that in October. In Marley Wood, 10 of 35 records were of ground hunting, and in north Oxford, where great tits had been few in October there were 131 records of ground feeding in a total of 189. December 1948 saw the establishment of ground feeding as the dominating habit in all the habitats: 50% of the records in Wytham Great Wood, 58% at Brightwell, 70% in Oxford.

In the first quarter of 1949 ground foraging predominated in the area as a whole, with 48, 40 and 46% of the records for the three months. In January the Wytham Great Wood birds showed a significant decrease in activity on the ground as compared with the previous month (23% of 35 records). Work in the Great Wood in February

Table 2. *Feeding activities of the great tit in Wytham Great Wood, June 1947–49*

	June 1947	June 1948	June 1949
Number of records	65	165	82
Percentage of records of ground feeding	0	2	1
Percentage of records of feeding between 0 and 24 ft.	85	66	65

and March was restricted, and only a few great tit records were made in these two months. At Brightwell there was a significant increase from February to March in the proportion of birds active at or over 20 ft.

In Wytham Great Wood in April 1949, 20% of 64 records were of birds feeding on the ground, and another 48% of the records were of activity between the lowest undergrowth and 19 ft. The defoliating caterpillars had hatched—on 18 April a density of 21·95 caterpillars per 100 leaves had been found in one oak—but the great tits, even as late as 26 April, were not determinedly seeking them. May was given to observations on the foods of nestlings. In June 1949 the height distribution of feeding great tits resembled that in June 1948 (Table 2).

In October and November 1949 the great tits of Wytham fed but little (7 and 7·5% of records) on the ground. 1949 was a year of abundant aphids (Table 1), in the Great Wood, and a light crop of beech-mast. As in 1947 the great tits fed much in sycamores (27 and 30% of records in the two months) and in oaks (11 and 20% of records) and not at all in beeches. In Brightwell and in Oxford the records of ground feeding in each month exceeded 50% of the total.

In December 1949 the winter routine of ground feeding was again generally established: 56% of the records from Wytham Great Wood, 51% of 189 records from Bagley Wood, and 81% in north Oxford. In January 1950, 20 of 28 records from the

Great Wood, and 57% of the records from the area as a whole were of birds foraging at ground level.

To sum up, great tits are ground-feeding birds in winter quarters and in the mid-winter months (December to March) in the areas where the species is resident. Great tits go up into the trees for the caterpillar harvest of early summer, work the lower woodland foliage in high summer, and in autumn feed high or low as supplies dictate.

(*b*) *The blue tit*

At all seasons of the year the distribution in height of feeding blue tits was characterized by its wide range. Visits to the modal feeding levels usually exceeded the visits to the levels next in frequency (but not necessarily nearest in level) by only a small percentage of the total for the month.

In February 1947 blue tits were feeding at all heights from the ground to more than 60 ft., 15–19 and 25–34 ft. being the levels most frequented. In March and in April, 10–19 ft. was the modal level; and in May, 10–24 ft. In June, many observations were made in north Oxford: there the blue tits were most active at low levels—76% of the records were of birds at less than 20 ft. In July and August foraging was fairly evenly dispersed between the lowest scrub and 34 ft.

In September 1947 the blue tits at Brightwell fed relatively more ($P < 0{\cdot}02$) at heights of 20 ft. and more than did the birds of the Great Wood; in the latter place there was significantly more foraging in the fruiting elders. In October this difference between the foraging habits of the blue tits of Brightwell and the Great Wood had vanished. The titmice of both localities differed significantly from the birds of north Oxford in the smaller proportion of ground feeding (one record of 70 in the Great Wood, nil of 44 at Brightwell, seven of 21 in Oxford).

In November 1947 the most frequented level in Wytham Great Wood was 30–34 ft., the proportion of birds at or over 20 ft. being 63%, a marked increase over the October proportion ($P < 0{\cdot}02$). In Oxford ground foraging by blue tits had almost ceased, and 45% of 40 records were of birds at more than 19 ft. In December 72% of the Wytham Great Wood records were of blue tits at or above 20 ft., 18% of them being birds at 50 ft. or more, a highly significant increase over the 3% of records at such heights in the November sample.

In January 1948, 20–24 ft. was the most frequented level in the Great Wood and also in the area as a whole. There was no feeding on the ground. In Wytham Great Wood 30% of the records were of birds at 50 ft. or more. February was remarkable in Wytham Great Wood for the even height distribution of feeding activity: in the seven stages between 10 and 45 ft. the percentages of records were 10, 10, 10, 11, 11, 11. Foraging at or above 50 ft. contributed only 11% of the records. At Brightwell the blue tits were active at much lower levels, 76% of records being less than 20 ft., as against 31% in the Great Wood. Oxford showed an intermediate distribution, with 54% of the feeding below 20 ft. There was little ground feeding anywhere.

In March 1948 blue tits in the Great Wood were evenly distributed between 20 and 44 ft. Only 17% of the records were of birds at less than 20 ft., a significant decrease from the degree of activity in the lower levels in February. But in Oxford the proportion of birds below 20 ft. had slightly increased. In April the level most frequented

was 15–29 ft. In Wytham Great Wood, whence the majority of the records came, the distribution of foraging activity through a wide range of levels had vanished, for the blue tits were deserting the higher twigs. This desertion of the upper levels continued in May: the modal foraging level in the Great Wood had fallen to 10–24 ft., and only 1% of the records were at 50 ft. or more. In the months of high summer the blue tits tended to forage lower and lower, the records of birds below 20 ft. in June, July and August 1948 being 41, 46 and 53% of the monthly totals. In July and August there were no observations of activity at or over 50 ft. Meanwhile, outside the Great Wood, blue tits fed at low levels in bushes and roadside weeds. In June, July and August the percentages of birds active at less than 20 ft. were 96, 65 and 81%. In and around Brightwell 29% of 83 feeding places recorded were on hogweed, *Heracleum sphondylium* L.

In September 1948 ground feeding (24% of 163) predominated among the blue titmice for the first time since observation began. This was the result of a very large crop of walnuts. At Brightwell 30 of 117 records (26%) were of birds on the ground, hacking into fallen nuts. There was no ground feeding in Wytham, but the titmice were in general in the lower levels, 55% of foraging being below 20 ft. In October the walnut harvest continued to affect the habits of the Brightwell blue tits; 66 of 214 records were of ground feeding. The effect of this temporarily super-abundant food supply on the routine of blue titmice is illustrated in Fig. 2. In Oxford, where the blue tits had arrived for the winter, there was also much ground feeding on fallen beech-mast (nine of 21 records). In Wytham Great Wood the beginning of a return to higher levels was seen; the percentage of birds at or over 35 ft. (23%) was the highest since March, and blue tits were seen foraging above the 50 ft. level for the first time since June. In Marley Wood the distribution of feeding activity was similar to that in the Great Wood. In both woods the birds were busy in elders and beeches.

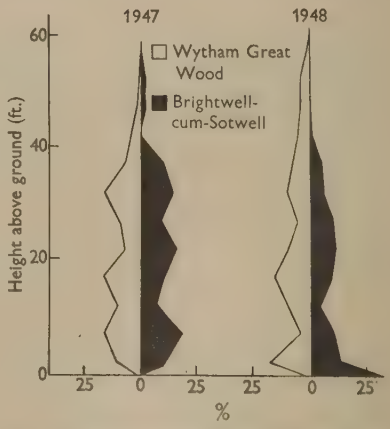


Fig. 2. Height-frequency distributions of the feeding stations of blue tits in Wytham Great Wood and at Brightwell, October 1947 and October 1948.

In November 1948 there were but slight changes in the feeding habits of the blue tits in the Great Wood. In Oxford ground feeding was still predominant (41% of 76 records). At Brightwell, with the end of the walnut harvest, there was less ground feeding. The blue tits were active in low shrubs and bushes, and so continued through the winter. In Wytham Great Wood blue tits maintained the tendency to feed at higher levels as the winter advanced. In December the percentage of birds feeding at or above 35 ft. had increased from 25% in November to 30%, with 8% of the records at 50 ft. or more—the largest proportion of activity at these heights since March. In north Oxford in December ground foraging had ceased.

In January 1949 the feeding activities of the blue tits of the Great Wood differed

a little from those of the previous month. The percentages of birds at or above 35 ft. (20%) and at or above 52 ft (4%) were both less than in December, and the proportion of birds below 20 ft. (59%) showed a marked increase in low-level feeding ($P < 0{\cdot}02$). In north Oxford there was a fairly even height distribution up to 55 ft.

In February the blue tits of Wytham Great Wood moved upward again. There was no feeding on the ground, only 18% of the observations were of birds at work at heights of less than 20 ft., 48% were at 35 ft. or more and 22% at 50 ft. or more. March in the Great Wood showed no significant differences from February, and April showed little difference from March, save that the proportion of birds foraging below 20 ft. was significantly less—10% as compared with 26%. While Wytham Great Wood showed a marked rise in feeding levels in the early spring months, in north Oxford there was a tendency for the blue tits to feed at lower levels as the spring advanced (Table 3).

Table 3. *Height distribution of feeding blue tits in north Oxford, 1949*

	January	February	March	April
Number of records	65	63	27	19
Percentage at or above 35 ft.	22	8	4	16
Percentage below 20 ft.	39	47	56	68

May 1949 was given to work on the food of nestlings. The few Wytham observations were of birds feeding high—11 of 18 foraging places were at heights of 35 ft. or more. The disposition of feeding blue tits in Wytham in June 1949, with 23% of the observations at or above 35 ft. and 32% below 20 ft. did not differ significantly from those observed in June 1948.

September 1949 saw most of the blue tits of the area feeding below 20 ft. Elder berries in Wytham and elder berries and pears at Brightwell attracted the birds to low levels. There was little ground foraging: the walnut crop was smaller than in 1948, and the nuts were thicker shelled and did not fall so soon. In October 1949 blue tits in Wytham Great Wood had begun to move upward. This general rise in feeding levels was continued until the end of the year (Table 4). Differences between October and

Table 4. *Height distribution of feeding blue tits in Wytham Great Wood, 1949–50*

	October	November	December	January
Number of records	170	166	106	193
Percentage at or over 50 ft.	4	2	10	7
Percentage at or over 35 ft.	15	13	32	17
Percentage below 20 ft.	53	44	29	58

November are not significant, but when December is compared with November, the increase in activity at or above 35 ft. and the decrease in activity below 20 ft. are both statistically significant. (In the increase in the proportion of birds feeding at or over 50 ft. $P < 0{\cdot}02$.) In December 1949 a sample of 372 records was obtained in Bagley Wood. The percentage of birds foraging below 20 ft. (42%) was significantly larger than the 29% in the Great Wood, but the proportion of activity at 35 ft. and above (25%) did not differ significantly from that in Wytham.

While the blue tits in the Great Wood showed a rise in feeding levels during the last months of 1949, the birds at Brightwell showed a descent, the proportions of

birds hunting below 20 ft. being 81% in October, 84% in November and 100% in December. In this last month 8 of 29 records were of ground feeding. There were few observations in Oxford before December. In that month 18 of 25 records were of birds below 20 ft.—a proportion significantly less than that at Brightwell as it is higher than that in the Great Wood.

In January 1950 there was a general drop in the height of the feeding blue tits in Wytham Great Wood. The percentage of birds at or over 35 ft. (18%) was significantly less than the 32% in December and the proportion of birds below 20 ft. (58%) was twice that in the previous month. A similar, but less marked drop was recorded in January 1949. At Brightwell, by contrast, there was a rise in general level; 11% of the birds observed were at work at 35 ft. or more, the first records at such heights since October. Records of feeding below 20 ft. were 82% of the total, a decrease in low-level feeding, as compared with the previous month of $P < 0{\cdot}02$. January of 1948 had shown a similar slight lift in height distribution. Oxford also showed a rise in feeding levels, with 28% of the observations of birds at or above 35 ft., as against 4% in December ($P < 0{\cdot}05$) and 32% at less than 20 ft. as against 72%, a statistically significant difference.

Feeding blue tits range through a diversity of heights. In the winter months especially they are scattered from the lowest shrubs to the tops of the highest trees. In the mid-summer months the highest levels are deserted. Only when there is an abundant harvest of fallen nuts or fruits do blue tits feed on the ground with any frequency.

(*c*) *The coal tit*

In 1947 coal tits were seen in numbers only in Wytham and in north Oxford. In March they were fairly evenly distributed between the ground (12% of all records) and 44 ft., with a few birds feeding up to 65 ft. In April 92% of the records were distributed rather less evenly between 5 and 39 ft.

In June 1947 the dispositions of feeding coal tits in Oxford and in Wytham Great Wood were very different. In Oxford 53 of 57 records were of birds at work below 20 ft. In the Great Wood 14 of 15 records were of birds at 20 ft. or more. In July there was a significant rise in the feeding levels of the Oxford coal tits, half the 18 records being of activity at 20 ft. or above. In the Great Wood the lift was even more remarkable, 22 of 25 observations being of birds between 35 and 69 ft., compared with two records out of 15 above 35 ft. in June. In September 1947, 25 of 26 records from the Great Wood were of birds at or above 20 ft., while in north Oxford 16 of 26 records were of birds at 19 ft. or less. In September, in the Great Wood, 88% of the records lay between the levels 20 and 44 ft.; in November 68% of the records were between these levels, and in December 62%.

In 1948 most of the records (700 out of 869) came from Wytham Great Wood; discussion will be confined to the results from this area. In January records were few. During the next eight months the levels 20 and 44 ft. contained a remarkably even percentage of the monthly records, varying between 62% in April and 84% in July (Table 5). There were minor differences from month to month, including general descents in April and in July and some very high-level foraging in August. The months of high summer showed a concentration of activities between 25 and 34 ft.—51% of

records in June, 51% in July and 54% in August. In October and November 1948 there was a fairly even dispersal of foraging between the ground and about 60 ft. In December there was much feeding on the ground (12 or 40 records) and hunting in the trees up to about 50 ft.

In 1949, 305 records were obtained in Wytham Great Wood. In January, 13 of 22 observations were of birds between 20 and 44 ft., and the rest at lower levels. March, April and June generally resembled the spring and summer of the previous year, having 78, 68 and 77% of the records between 20 and 44 ft. But April 1949 differed from April 1948 in a general rise in the foraging levels, as compared with March. In October 66% of 52 observations were of birds between 20 and 44 ft.; by November the proportion within these levels had dropped to 58%, and in January 1950 it was 35%. In January 1950, as in January 1949, the bulk of the records outside the 20–44 ft. limits came from lower heights; but there was no ground feeding. In December 1949 a sample of 154 observations was obtained in Bagley Wood. Of the records 38% came from between the 20 and 44 ft. levels, and 57% from below. These figures are comparable with those obtained in Wytham Great Wood in December 1948 and January 1950.

Table 5. *Coal tit. Wytham Great Wood 1948. Percentages of records of feeding activity at different levels*

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
20–44 ft.	(57)	71	70	62	82	83	76	84	65	49	39	37·5
> 44 ft.	—	13	12	12	2	2	2	10	4	22	24	10
< 20 ft.	—	15	17	24	15	15	21	4	31	28	39	52

The general disposition of feeding coal tits in Wytham is one of fairly high level activity in spring and summer, with a wider dispersal in autumn through a big range of heights and a drop to lower levels in mid-winter.

(*d*) *The marsh tit*

The marsh tit is not a bird of gardens and orchards. Of the 1819 records available 88% were made in Wytham Great Wood, 6·7% in Marley Wood and 2·5% in Bagley Wood. The marsh tits of Wytham were much reduced by the hard weather of early 1947. Records were few for the first half of that year. Throughout the period of observation the uniformity of the height distribution of the feeding marsh tits was in marked contrast to the changing dispositions of the great tit. In 21 of the 23 months for which there are adequate figures more than 50% of the feeding records were of birds foraging between < 5 and 19 ft.; in 16 of the 23 months more than 60% of the records lay within them, with maxima of 40 of 45 records in October 1947 and 38 of 44 records in November 1949. Of the records collected in Marley Wood in 1948, 81% in May, 100% in June, 92% in August and 68% in November were within the limits < 5 to 19 ft.

In the winter 1947–48 the proportion of marsh tits recorded as feeding above 19 ft. increased significantly from October to November. There was then no marked change in this proportion until a slight drop in February and a further drop in March. When the 50% of 'high' birds in January is compared with the 29% in March, the decrease

is sufficient to give $P<0{\cdot}02$. Through the spring and summer months of 1948 the general height distribution of feeding birds varied only a little. May saw a partial desertion of the lower levels. The percentage of birds feeding below 15 ft. (36%) was less than the 54% of April ($P<0{\cdot}05$) and less than the 52% of June ($P<0{\cdot}02$). This slight rise to higher levels coincided with the month of greatest abundance of defoliating caterpillars. In July and August there was a little ground feeding, and in August and September the population fed at its lowest levels for the year, 63 and 62% of the records being below 15 ft. In October the feeding level had begun to rise again, and it rose much more sharply in November, when 58% of the records were of birds at 20 ft. or more. Hunting for beech-mast may have accounted for some of this high-level feeding, just as the hunt for fallen mast may have brought some birds to the ground. (There was practically no ground feeding in the mastless autumn of 1947.) In December 1948 there was an unusually large amount of ground feeding, 23 records of 104. Of these 23 records of marsh tits on the ground, 15 were noted as under beech trees.

In January 1949, 56% of 48 records were of birds between <5 and 19 ft., and there were 8 observations of hunting on the ground. In March the percentage of records between <5 and 19 ft. had risen to 70%. April showed an increase in the proportion of birds feeding above 20 ft., but the figures are not sufficient to show statistical significance. In June 76% of the records were between <5 and 19 ft., and no birds hunting on the ground or above 30 ft. The autumn of 1949 showed a concentration of marsh tits below 20 ft., with very little ground feeding. The beech-mast crop of 1949 was markedly smaller than that of 1948. In December 1949 a sample of 47 records was made in Bagley Wood; 43% of the observations were of birds foraging between <5 and 19 ft., and 15% were of birds on the ground. There are only 18 Wytham records for this month; the proportion of birds between <5 and 19 ft. (13 of 18) differs from the proportion within these limits in Bagley Wood ($P<0{\cdot}05$). But the figures obtained in Bagley Wood in December 1949 do not differ from those collected in the Great Wood in December 1948.

January 1950 closely resembled January 1949 in the disposition of feeding marsh tits. The percentages of records of ground feeding and of foraging between <5 and 19 ft. were 19 and 58% as against 17 and 56% in 1949.

The marsh tit has the most clearly defined height-distribution of the four titmice. It is the titmouse of the shrub layer and the lowest limbs of big trees.

(*e*) *The long-tailed tit*

Since long-tailed tits were greatly reduced in numbers by the frosts of early 1947, only casual records of their activities were obtained during the rest of that year. Out of the breeding season long-tailed tits seem to be more nomadic in their habits than the other titmice. Long-tailed tits showed a considerable range of feeding levels. They were rarely recorded as foraging on the ground and not often in the highest twigs (Table 6). In the 13 months for which adequate figures are available (Table 7), more than 50% of the records were at or over 20 ft. in 10 months; more than 60% in seven; and less than 40% in one only, June 1948.

In Marley Wood in 1948, June with 94% of feeding records at less than 20 ft.

showed the least general feeding height recorded, and August with 70% of the observations at or over 20 ft. showed an intensity of upper levels foraging only twice surpassed in the Great Wood. In Bagley Wood in December 1949, 22 of 26 records (86%) were at 20 ft. or more; none was over 44 ft.

The long-tailed tit is, in general, a hunter in the top of the shrub layer and the lower strata of the woodland canopy.

Table 6. *Records of feeding at or above and below the 50 ft. level in blue, coal and long-tailed tits, 1948 and 1949*

	Blue tit	Coal tit	Long-tailed tit
Records of feeding at or above 50 ft.	220	63	22
Records of feeding below 50 ft.	2738	942	555
Total	2958	1005	577

χ^2 values: blue tit : long-tailed tit, −9·96; coal tit : long-tailed tit, −4·37; blue tit : coal tit, less than 2.

Table 7. *Percentages of long-tailed tits feeding at or above the 20 ft. level*

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1948	—	67·5	65	40	—	16	72·5	52·5	96	—	69	52
1949	40	—	—	—	—	—	—	—	—	69	61	—
1950	57·5			—					—			

INTER-SPECIFIC COMPARISONS

A survey has been made of the height-distribution of food-seeking activity in each species. The survey suggests that a mechanism of ecological separation exists in differences of vertical distribution. But it is in the single habitat, rather than over several square miles of varied country, that interspecific competition may be actual rather than potential; and in the single habitat comparisons may be made with most reality. The first basis of comparison in the discussion which follows is in the proportions wherein birds of two species were feeding at or above, and below, 20 ft. This level was chosen for two reasons. In many months, and in more than one species, the 20 ft. level patently divided an abundant from a scanty distribution. In addition, and perhaps in explanation of this fact of observation, the dominant species of the 'shrub layer' (blackthorn, elder, hazel, sallow) appear largely as specimens something under 20 ft. tall. The 20 ft. level is, therefore, a rough boundary between the 'shrub layer' and the canopy.

In the first four months of the survey the figures are not separable into the localities of collection. Practically none of the February records came from Wytham; the woods were almost empty of titmice by the end of that most rigorous month (Gibb 1950). In February 1947, despite the snow cover which often prevented the great tits from feeding on the ground, blue tits were recorded feeding at or above 20 ft. significantly more frequently than were great tits. In March and in April blue tits continued significantly more active in the higher levels than were great tits, and were significantly less often recorded foraging on the ground. In these two months coal tits showed relatively more activity at or over 20 ft. than did great tits in March ($P < 0{\cdot}02$) and relatively less feeding on the ground than did great tits in April ($P < 0{\cdot}02$). In May 1947 blue tits were still relatively more abundant at or above the 20 ft. level than were great tits, but the difference was much less ($P < 0{\cdot}05$). This reduction in the difference

between the feeding habits of great and blue tits coincided with the upward movement of the great tits in search of defoliating caterpillars. In this month coal tits did not differ from blue tits in height distribution, but fed significantly more often in the higher levels than did great tits.

(*a*) *Wytham Great Wood*

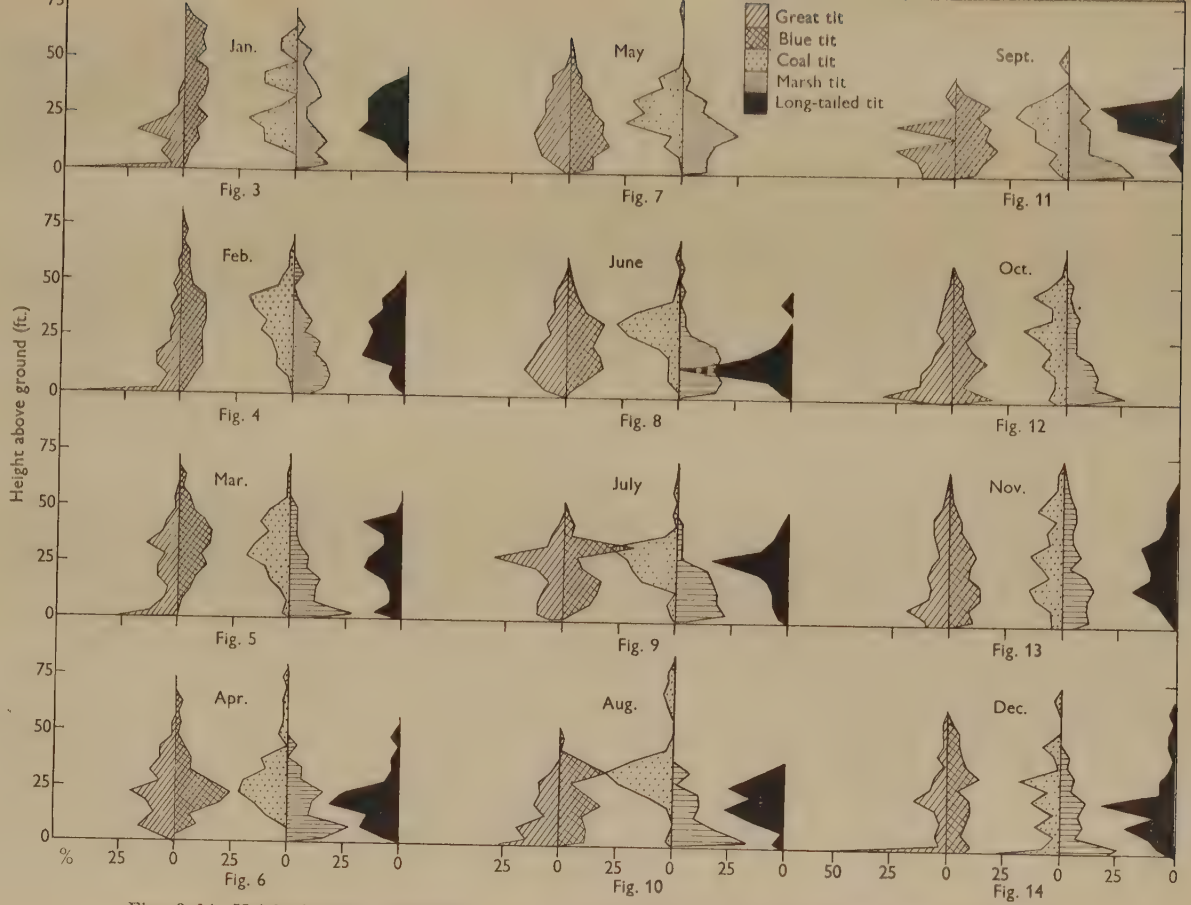
Wytham Great Wood has been selected for discussion in detail for two reasons: all five species of titmice, and also some willow tits, were regularly met there, and the numbers of records for all species greatly exceeded those from any other site. It has already been suggested that difference in height distribution is not the only possible mechanism of ecological separation among species which live intermingled. Birds may feed in trees of different species, or in different parts of the same trees, and the discussion of the feeding behaviour of the Wytham titmice is extended to include these two possibilities.

In October 1947 the number of coal tit records from Wytham Great Wood was too small to give data comparable with those for the other three parids. There was no difference between the height distributions of great and blue tits, but both species were feeding significantly more in the higher levels than were marsh tits. In November all four species were adequately sampled. There was no important difference in the vertical distributions of great and marsh tits, but blue tits were significantly more active in the higher levels than these two species, and coal tits were relatively more numerous at and over 20 ft. than were blue tits ($(P < 0{\cdot}02)$. In December the dispositions of great and marsh tits had not much altered. Blue and coal tits were both significantly more active in the higher levels. The blue tit population had shifted a little upward; there was no significant difference in the degrees of activity of blue and coal tits above the 20 ft. level.

In January 1948 (Fig. 3) there was still no difference between blue and coal tits in the general occupation of the higher levels. But now great tits with 22 of 49 records as the proportion of ground-feeding were significantly more abundant below 20 ft. than marsh tits. Marsh tits in turn were significantly more active in the shrub layer (below 20 ft.) than blue tits. In this month long-tailed tits did not differ markedly from blue or coal tits in the proportion of feeding activity above 19 ft.

In February 1948 (Fig. 4) the four Paridae were yet more sharply separated. Great tits fed at the lowest level with 41 % of all effort on the ground, significantly exceeding marsh tits in the proportion of birds below 20 ft. Marsh tits were the birds of the shrub layer being significantly more numerous than blue tits below 20 ft. Blue tits came next in the ascending order, and coal tits highest of all: the percentage of coal tits at or over 20 ft. was significantly greater than the percentage of blue tits. The vertical distribution of long-tailed tits closely resembled that of blue tits. In March (Fig. 5) conditions were little altered, save that there was now no significant difference between the proportions of blue and of coal tits foraging at or above 20 ft.

In April (Fig. 6) came a sudden change. The great tits had gone upward, leaving the ground, and did not now differ in feeding levels from blue tits. Marsh and long-tailed tits were the species of the lower levels. Coal tits differed ($P < 0{\cdot}02$) from great tits in the higher proportion of birds hunting at or above 20 ft.; they were a little, but



Figs. 3–14. Height-frequency distributions of the feeding stations of titmice in Wytham Great Wood, 1948.

not significantly, higher than blue tits. In May (Fig. 7) conditions were not much altered, save that coal tits had moved notably upward, and differed highly significantly from the other three parid species in the proportion of birds recorded at over 19 ft. Great tits slightly exceeded marsh tits in the relative numbers of birds in the upper levels ($P = 0{\cdot}05$), but there was no significant difference in the dispositions of blue and marsh tits. These disappearances or reductions of ecological separations coincided with the summer caterpillar outbreak of 1948. The plague was severe, many oaks being completely defoliated before the end of May.

In June 1948, the caterpillar abundance being over (by 8 June the caterpillars per 100 leaves of oak in two trees were 0·66 and 2·55, as against 48·2, 49·5 and 15·2 caterpillars per 100 leaves on 7 May) the ecological separation of the titmice reappeared (Fig. 8). The coal tit was the species most strongly represented in the upper levels, with blue tits significantly less abundant there. Great tits were more frequent below 20 ft. than were blue tits, and marsh and long-tailed tits were more active in the lower levels than were great tits. The differences between great tits and blue tits, and between great tits and long-tailed tits were both statistically significant (i.e. $P < 0{\cdot}01$). In the comparison of great and marsh tits, $P < 0{\cdot}02$). In July (Fig. 9) coal tits still showed the biggest proportion of birds active at or above 20 ft., and marsh tits still the smallest. Long-tailed tits had risen suddenly; the proportion of the sample above 19 ft. did not differ significantly from the proportion in coal tits. The sudden rise in hunting level of great tits in this month has been already mentioned. The cause of this activity in the canopy, which made equal the proportions of the blue and great tit samples above and below the 20 ft. level, could not be ascertained. There remained a significant difference between blue and great tits in the higher proportion of the latter species feeding on the ground.

In August (Fig. 10) coal tits were still more numerous in the higher levels than any other species. Blue and long-tailed tits came next, differing significantly from both great and marsh tits in percentages of birds over 19 ft. There was no difference between the proportions of great and marsh tits recorded below 20 ft., but there were significantly more great tits on the ground. In September (Fig. 11) there was no difference between the percentages of birds below 20 ft. in the blue, great and marsh tit records, but the proportion of great tits hunting on the ground slightly exceeded ($P < 0{\cdot}05$) the proportion of ground-feeding blue tits. Coal tits were at work at slightly higher levels than the other parids, differing significantly from great and marsh tits. Long-tailed tits were now feeding notably higher than the other species, 24 of 25 records being of birds at or above 20 ft. In October 1948 (Fig. 12) coal tits were significantly more active in the higher levels than the other species, and blue tits significantly higher than great and marsh tits. No long-tailed tits were seen in Wytham. In November (Fig. 13) there were no very striking differences in height distributions. Great tits were at a rather lower level than blue tits ($P < 0{\cdot}05$) and coal tits ($P < 0{\cdot}02$). Long-tailed tits showed the highest percentage (69%) of feeding records at heights of over 19 ft. This autumnal period of reduced ecological separation coincided with an abundant beech-mast harvest, and a notable gathering of titmice around the beeches. In December (Fig. 14) blue tits were the species most active above 19 ft. (59% of records). Long-tailed and coal tits were also busy in the higher levels, but

with ground foraging contributing 30% of the coal tit records, that species differed significantly from both blue and long-tailed titmice. Great tits, with ground feeding in half the month's observations, differed significantly from both coal and marsh tits.

In January 1949 there was still some gleaning under beeches, and no very marked ecological separations. Marsh and great tits did not significantly differ, nor did blue, coal, marsh and long-tailed tits. Blue tits showed significantly less ground-feeding than did great tits, and coal tits significantly more birds at or above 20 ft. than great tits did. February records were few. In March blue, coal and long-tailed tits were feeding significantly more above the 20 ft. level than were great tits. In 1949 the 'caterpillar outbreak' was a little later and not quite so large as in 1948. In April considerable ecological separations were still in force. Blue and coal tits were feeding significantly higher than great and marsh tits, and the proportion of ground feeding in great tits exceeded the proportion in marsh tits ($P < 0{\cdot}05$).

In June 1949, the caterpillar abundance being ended, the dispositions resembled those of June 1948. Coal tits were most frequently found at or above 20 ft., with blue tits next in order, great tits lower than blue tits and marsh tits showing the highest proportion of birds active in the 'shrub layer'.

The height distributions of the titmice in October 1949 resembled those of October of the previous year. Coal tits showed the greatest activity at or above 20 ft., blue tits being significantly less frequent in the upper levels than coal tits, and significantly more frequent there than either great tits or marsh tits. Great tits were more active on the ground than marsh tits ($P < 0{\cdot}02$). The hunting levels of long-tailed tits were similar to those of coal tits. November 1949 repeated the conditions of November 1948. Blue, coal and long-tailed tits did not differ in the proportions of records at or above 20 ft., and all showed a significantly greater activity in the 'high levels' than did great and marsh tits. Marsh tits fed rather less on the ground than did great tits ($P < 0{\cdot}05$). December 1949 showed much the same situation as November, but the difference between the amount of ground foraging by great tits and marsh tits had significantly increased. In January 1950 the same general dispositions of feeding birds continued—blue, coal and long-tailed tits fairly high, marsh tits in the 'shrub layer' and great tits largely on the ground.

After the discussion of the height distributions of feeding activities, possible preferences of different species of titmice for different trees must be considered. No species of tree in the wood went unvisited, but four species and one group of species were worked far more intensively than the rest: these were ash, elder, oak, sycamore and 'conifers'. Table 8 shows the frequencies of visits by the five species of titmice to these five feeding places, and also the total numbers of trees visited, data being massed for the quarters of the year. The results are shown graphically in Fig. 15, in which it is seen that there were differences in the utilization of the five most frequently visited trees by the five species of birds. χ^2 tests were made, comparing each species with every other, of the statistical significance of these differences. Table 9 shows the results of these calculations, with a summary below, showing the number of quarters in which each species was significantly ($P < 0{\cdot}01$) more often in each of the five trees than any one of its related species. A titmouse haunting one tree more frequently than the other

four species in every quarter would score a total of 16 'predominances'; and this the coal tit in conifers in fact did.

Fig. 15 and Table 9 show that, in Wytham Great Wood, of four members of the genus *Parus* the blue tit was the titmouse of oaks, the great tit the titmouse of sycamores, the coal tit the titmouse of conifers and the marsh tit the titmouse of elders.

Table 8. *Records of feeding activity of titmice in certain trees. Wytham Great Wood, 1947–50*

	Total	Jan.–Mar.	Apr.–June	July–Sept.	Oct.–Dec.
BLUE TIT					
Ash	294	72	108	20	94
Elder	259	38	29	43	149
Oak	1200	443	301	97	359
Sycamore	585	224	100	34	227
'Conifers'	260	48	78	32	102
Total trees	3484	1083	814	320	1267
GREAT TIT					
Ash	84	9	39	7	29
Elder	194	42	31	23	98
Oak	393	46	162	50	135
Sycamore	415	62	116	94	143
'Conifers'	91	22	28	20	21
Total trees	1642	247	538	236	621
COAL TIT					
Ash	113	39	33	13	28
Elder	31	3	3	4	21
Oak	231	80	69	21	61
Sycamore	99	42	17	7	33
'Conifers'	628	115	191	170	152
Total trees	1201	308	334	220	339
MARSH TIT					
Ash	103	31	23	14	35
Elder	293	77	68	28	120
Oak	372	120	97	36	119
Sycamore	187	45	31	25	86
'Conifers'	70	20	21	11	18
Total trees	1448	352	340	176	580
LONG-TAILED TIT					
Ash	64	10	8	5	41
Elder	47	24	3	5	15
Oak	112	59	9	16	28
Sycamore	134	70	16	15	33
'Conifers'	116	24	6	52	34
Total trees	620	231	67	123	199

The position of the long-tailed tit was less clear, but it seemed to be a bird of ashes, sycamores and conifers rather than oaks and elders. The long-tailed tit was the only species showing a marked seasonal change in choice of feeding trees. It was predominant in ashes only in the last quarter of the year. In sycamores it showed six predominances out of a possible eight in the first half of the year and only one in the second: in conifers it showed one predominance in the first half of the year and six out of a possible eight in the second. The disappearance of the predominance of marsh

tits over blue tits in elders during the third quarter, and the appearance of blue tit predominances over coal and long-tailed tits at the same season reflected the blue tit's fondness for elder berries.

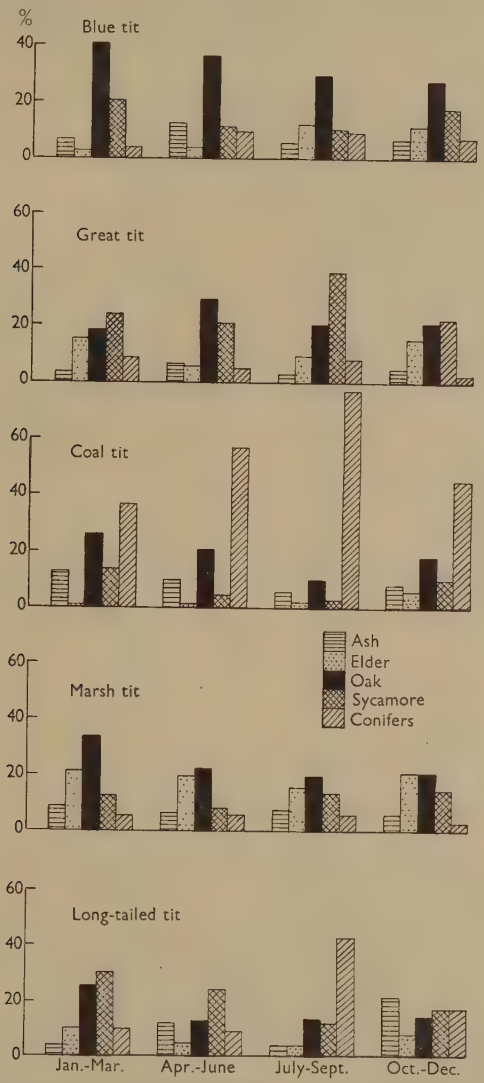


Fig. 15. Comparative frequencies of feeding visits of titmice to certain species of tree in Wytham Great Wood in the four quarters of the year, 1947 to 1950.

A third possible separation in feeding habits is in foraging in different parts of the trees—among leaves, along twigs or branches or on the trunks. Observations on this subject have been assembled in the same manner as those on utilization of different trees. Table 10 shows the frequencies of records of hunting by the five species of

Table 9. *Values of χ^2 in comparisons of frequencies of feeding visits to different trees in Wytham Great Wood, 1947–50. Below—the 'predominances' in the different trees*

Quarters of the year ...	Ash I	Ash II	Ash III	Ash IV	Elder I	Elder II	Elder III	Elder IV	Oak I	Oak II	Oak III	Oak IV	Sycamore I	Sycamore II	Sycamore III	Sycamore IV	Conifers I	Conifers II	Conifers III	Conifers IV
Blue tit:																				
Great tit	—	12·11	—	5·9	—	—	—	—	43	6·88	5·82	8·99	—	—	—	—	—	8·54	—	15
Coal tit	—	—	—	—	5·28	6·2	7·93	8·71	22·7	29	25·5	14·8	11·6	13·85	10·7	13·18	—	—	—	—
Marsh tit	—	10·1	—	—	—	—	—	—	5·8	6·9	5·62	12·61	10·83	—	—	—	—	—	—	16
Long-tailed tit	—	—	—	—	—	—	9·16	—	19	15·05	13·58	17·9	—	—	—	—	—	—	—	—
Great tit:																				
Blue tit	—	—	—	—	63	—	—	5·92	—	—	—	—	—	21	66·6	6·88	8·04	—	—	—
Coal tit	—	—	—	—	47·7	13	13·5	18·75	—	13·23	—	—	11·81	42·2	89	25·8	—	—	—	—
Marsh tit	—	—	—	—	—	—	—	—	—	—	—	—	15·1	23·2	5·38	13·1	—	—	—	—
Long-tailed tit	—	—	—	—	4·56	—	—	8·54	—	8·39	—	5·52	—	—	34·2	—	—	—	—	—
Coal tit:																				
Blue tit	12·49	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	249	276	250·5	271
Great tit	17·6	—	20·78	3·8	—	—	—	—	3·86	—	6·1	—	—	—	—	—	59·2	371	218·2	256
Marsh tit	3·95	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	107	202	198·6	248
Long-tailed tit	11·05	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	50	519·5	42·2	42·3
Marsh tit:																				
Blue tit	—	—	—	—	133·5	83·5	—	25·5	—	—	—	—	—	—	—	—	—	—	—	—
Great tit	6·19	—	5·7	—	—	42	—	4·85	17·43	—	—	—	—	—	—	—	—	—	—	—
Coal tit	—	—	—	—	67·4	64·5	39·3	34·55	5·12	5·6	8·44	—	—	4·14	16·02	4·9	—	—	—	—
Long-tailed tit	4·89	—	—	—	12·72	9·37	10·33	17·9	—	6·46	—	—	—	—	—	—	—	—	—	—
Long-tailed tit:																				
Blue tit	—	—	—	35·4	20	—	—	—	—	—	—	—	11·7	7·74	—	—	13·1	—	70	16·65
Great tit	—	—	—	49	—	—	—	—	—	—	—	—	—	—	—	—	—	—	57·3	45·3
Coal tit	—	—	—	39·96	25·4	4·86	—	—	—	—	—	—	14·7	27·1	10·64	5·49	—	—	—	—
Marsh tit	—	5·12	—	36·1	—	—	—	—	—	—	—	—	26·88	11·84	—	—	—	—	56·3	46·6

'Predominances' (probability of 0·01)

Blue tit		2				3				13				5				3		
Great tit		—				6				2				11				1		
Coal tit		4				—				—				—				16		
Marsh tit		—				12				2				1				—		
Long-tailed tit		4				2				—				7				7		

titmice in four different hunting places: leaf, twig, branch (and limb) and trunk. The data are masses for the four quarters of the year. Fig. 16 illustrates these data; Table 11 gives the results of calculations of significance of frequency differences, with a summary showing the number of quarters of the year where in each species of titmouse was predominant at work in any one hunting place over another species.

Table 10. *Utilization of different feeding places in the four quarters of the year. Wytham Great Wood, 1947–50*

	Total	Jan.–Mar.	Apr.–June	July–Sept.	Oct.–Dec.
Blue-tit					
Leaf	421	20	218	56	127
Twig	1884	763	257	153	711
Branch	209	64	37	9	99
Trunk	140	59	1	12	68
Total	2654	906	513	230	1005
Great tit					
Leaf	193	3	118	28	44
Twig	746	175	150	108	313
Branch	169	24	40	17	88
Trunk	66	11	9	7	39
Total	1174	213	317	160	484
Coal tit					
Leaf	170	25	48	46	51
Twig	624	199	175	81	169
Branch	122	31	24	11	56
Trunk	64	8	7	16	33
Total	980	263	254	154	309
Marsh tit					
Leaf	143	1	87	20	35
Twig	570	204	84	55	227
Branch	206	74	24	20	88
Trunk	77	26	12	7	32
Total	996	305	207	102	382
Long-tailed tit					
Leaf	12	—	5	6	1
Twig	481	162	33	114	172
Branch	16	10	2	2	2
Trunk	9	2	1	1	5
Total	518	174	41	123	180

Differences were less pronounced than in the visitation of different trees, but the long-tailed tit was markedly the titmouse of twigs, with fifteen out of sixteen possible predominances. The marsh tit, with nine out of a possible sixteen predominances, was the titmouse of branches, and the coal tit, with eight out of a possible sixteen, showed the highest number of predominances in leaves and needles. The blue tit was more often predominant as a hunter among leaves and along twigs than as a searcher of branches and boles. It has earlier been shown that the great tit was often predominant on the ground.

Fig. 16 shows that the proportionately small amount of leaf feeding by coal tits in the second quarter of the year, in comparison with the other four species, was not attributable to a decrease in leaf feeding by coal tits but to a very marked increase in

leaf searching by the other titmice. This increase in leaf searching coincided with the increase in the populations of leaf-feeding caterpillars in the early summer. The high frequency of leaf hunting by coal tits in the first and last quarters of the year resulted from the species' preference for coniferous trees. In the autumn of 1949 coal tits were active in probing between the thick-clustering keys of ash. Odum (1942) found con-

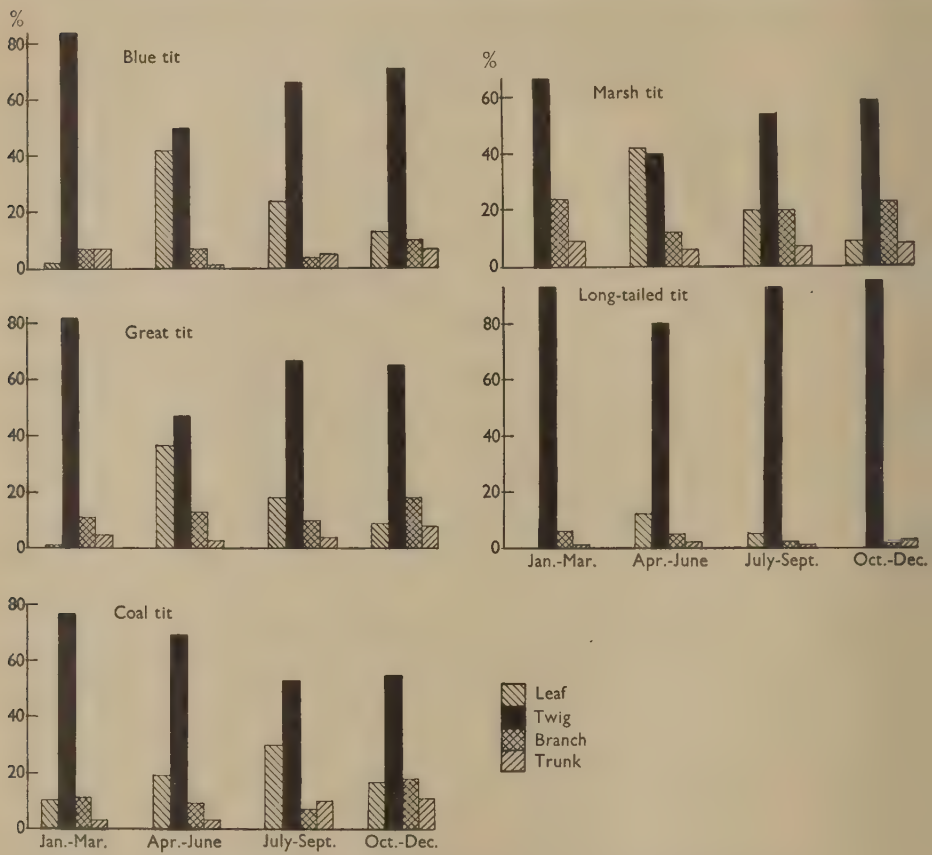


Fig. 16. Comparative frequencies of feeding visits of titmice to different parts of trees, Wytham Great Wood in the four quarters of the year, 1947 to 1950.

siderable seasonal variation in the feeding places of *Parus* (*Penthestes*) *a. atricapillus*. Fig. 16 also shows how little the flush of leaves in early summer affected the feeding place of the long-tailed tits.

It is not suggested that all the mechanisms of ecological separation between titmouse species have been explored. But it has been shown that in Wytham Great Wood the five species of titmouse there living intermingled are separated in three different ways —in foraging at different heights, in searching of different trees and in seeking food in different parts of those trees. Not all the species are separable all the time; but no two are identical in their feeding behaviour.

Table 11. *Values of χ^2 and 'predominances' in comparisons of frequencies of feeding visits to different parts of trees. Wytham Great Wood, 1947–50*

Quarters of the year ...	Leaf				Twig				Branch				Trunk			
	I	II	III	IV	I	II	III	IV	I	II	III	IV	I	II	III	IV
Blue tit:																
Great tit	—	—	—	4·03	—	—	—	6·22	—	—	—	—	—	—	—	—
Coal tit	—	41·9	—	—	10·25	—	7·5	28·45	—	—	—	—	4·53	—	—	—
Marsh tit	4·73	—	—	—	42·2	5·16	4·53	16·4	—	—	—	—	—	—	—	—
Long-tailed tit	3·93	14·45	120·7	21·1	—	—	—	—	—	—	—	14·82	8·75	5·3	4·38	4·21
Great tit:																
Blue tit	—	—	—	—	—	—	—	—	3·99	6·82	6·86	20·6	—	11·53	—	—
Coal tit	—	22·9	—	—	—	—	7·51	7·9	—	—	—	—	—	—	—	—
Marsh tit	—	—	—	—	14·8	—	7·6	—	—	—	—	—	—	—	—	—
Long-tailed tit	—	10	10·41	15·1	—	—	—	—	—	—	9·36	32·6	4·73	—	—	12·16
Coal tit:																
Blue tit	32·7	—	—	—	—	24·6	—	—	5·6	—	—	17·2	—	11	—	5·16
Great tit	13·59	—	—	9·78	—	29·95	—	—	—	—	—	—	—	—	4·16	—
Marsh tit	24·65	—	—	8·5	—	37·3	—	—	—	—	—	—	—	—	—	—
Long-tailed tit	16·12	—	27·95	29·92	—	—	—	—	4·49	—	4·64	31·8	—	—	10·93	6·01
Marsh tit:																
Blue tit	—	—	—	—	—	—	—	—	64·8	—	20·5	41·5	—	25·9	—	—
Great tit	—	—	—	—	—	—	—	—	13·78	—	4·16	—	21·4	—	—	—
Coal tit	—	29·4	—	—	6·9	—	—	—	14·65	—	8·95	—	—	—	—	—
Long-tailed tit	—	13·1	11·83	15·05	—	—	—	—	21	—	20·58	44	10·89	—	5·95	6·01
Long-tailed tit:																
Blue tit	—	—	—	—	9·39	13·36	30·6	46·4	—	—	—	—	—	—	—	—
Great tit	—	—	—	—	10·25	16·1	26·2	64	—	—	—	—	—	—	—	—
Coal tit	—	—	—	—	22·6	—	52·6	89·5	—	—	—	—	—	—	—	—
Marsh tit	—	—	—	—	42·4	22	45	78·3	—	—	—	—	—	—	—	—

'Predominances' (probability 0·01)

Blue tit	4		5		1		1
Great tit	4		4		5		2
Coal tit	8		3		2		2
Marsh tit	4		1		9		3
Long-tailed tit	—		15		—		—

(*b*) *Brightwell-cum-Sotwell*

In the village of Brightwell-cum-Sotwell the summer titmouse population was small. The winter population consisted of many great and blue tits and a few coal tits.

In the autumn of 1947 there was no difference in the height dispersal of great and blue tits in September. In October and November blue tits were significantly more active at or above 20 ft. In December there were few observations of either species above 19 ft., but great tits were significantly the more occupied upon the ground.

In January 1948 there were few great tit observations, but blue tits were tending to seek higher levels, so that in February blue tits were more active ($P < 0{\cdot}02$) than great tits at or above the 20 ft. level. There were no significant differences between the two species in March.

In July 1948 there were more blue tits than great tits at work above 19 ft. ($P < 0{\cdot}05$), and in August significantly more great tits were foraging on the ground. In the three autumn months, September, October, November, with the great harvest of walnuts, no marked differences were found between the two species. In December 1948 and in January and February 1949 great tits were significantly more active on the ground than were blue tits. In the two latter months there was also statistical significance in the larger percentages of blue tits above 19 ft. In March 1949 there were still significantly more great tits than blue tits feeding on the ground, but the great tits had extended their feeding range upward, and there was no important difference in the hunting activities of the two species above 19 ft.

In the four months October 1949 to January 1950 there were no significant differences in the proportions of great and blue tit records at 20 ft. and more, but in every month relatively more great tits were feeding on the ground (P in the first three months 0·01, in the fourth 0·05).

In 1947 there was no walnut crop, and as soon as the elder berries were eaten (October) ecological separation appeared between blue and great tits. In 1948 the elder harvest was followed by a bumper crop of walnuts, and there was no ecological separation between the two species until December. In 1949 there was an average walnut crop. In October and November (there were no September observations) there were no differences in high-level feeding but there was more ground-feeding in great tits than in blue tits. It would seem that the effect of the walnut harvest was to make some great tits work upward in search of nuts still on the twigs, and that many shattered nuts lying below the trees would bring the blue tits down to feed on them.

The number of coal tits observations from Brightwell was too small for more than a general statement. In the second half of 1947 and the first quarter of 1948 coal tits at Brightwell were more active than blue tits at or above 20 ft. In the first quarter of 1949 there was no significant difference from blue tits.

(*c*) *North Oxford*

In north Oxford the titmouse population was greatly augmented in winter, blue and great tits appearing in numbers. In 1947 figures sufficient for the comparison of these two species were obtained in June, July and September to December. In all these months, save October, blue tits were significantly the more active at heights of 20 ft. and above. In October, with some beech-mast, there was no significant difference

between the two species, either in the proportions of activity above and below 20 ft. or in relative frequency of ground-foraging.

From January to May 1948 blue tits showed a consistently higher proportion of records of birds feeding at or above 20 ft. than did great tits, and very much less activity on the ground. In September and October 1948 with a heavy crop of beech-mast there were no significant differences between blue and great tits either at 'high-levels' or on the ground. In November 1948, though many blue tits were still seeking fallen beech-mast, the proportion of ground-feeding birds was now significantly less than in the great tit and the proportion of 'high-level' birds was significantly more. In December 1948 there were no blue tits foraging on the ground as compared with 70% of the great tit records. January to March 1949 saw blue tits in north Oxford consistently more active in the higher levels than the great tits and far less active on the ground.

In the following winter there were few blue tits before December 1949: in that month and in January 1950 blue tits were again proportionately more frequent at or above 20 ft. and great tits more frequent upon the ground.

In general the height distribution of feeding coal tits in north Oxford differed little from that of the blue tits. May 1947 when coal tits were feeding unusually low was an exception to this generalization.

(*d*) *Bagley Wood*

In one month, December 1949, the titmice of Bagley Wood were sampled. The general relationship between four of the five species resembled the usual mid-winter situation in Wytham Great Wood. Great tits were feeding at the lowest levels. The proportion of records from below 20 ft. and the percentage of ground-feeding activity were significantly greater than in all the other species. Blue tits showed a significantly larger proportion of birds hunting at or above 20 ft. than did two other members of the genus *Parus* (great tit and coal tit) and some excess over the marsh tit ($P < 0{\cdot}05$). Long-tailed tits were at the highest general level, significantly exceeding the other titmice in the proportion of records at or over 20 ft. Marsh tits and coal tits did not differ significantly in their distributions about the 20 ft. level, and occupied an intermediate position between the great tits and the blue tits.

DISCUSSION

The general ecological relationship between the titmice of English woodlands is very similar to that described by Lack (1947) in *Darwin's Finches of the Galapagos*: '...ecological divergence has mainly taken the form of difference in food habits, in which case the species are not forced to occupy separate habitats, but can exist side by side.' It has been shown that in an area of English country the species of titmice are ecologically separated by their feeding habits; that each species has its characteristic height distribution, fixed or varying seasonally; that each species has its favoured foraging trees, and a tendency to seek its food in different parts of those trees; and that no two species are identical or even consistently similar in their food-seeking behaviour.

Palmgren (1930) found that in southern Finland, great, blue and long-tailed tits were the titmice of deciduous trees, and coal tits the titmice of spruce. In Holland, Kluijver (1951) describes great tits as preferring 'broadleaved deciduous woods to conifers'.

In July and August 1948, Snow (1949) investigated the height distribution of feeding titmice in the woods near Uppsala, Sweden. He found that

> The great tit fed at all heights, and showed a slight preference for spruce. It dominated the mixed flocks, usually keeping high.
>
> The blue tit was constantly high. The high proportion of records from pine was due to the preponderance of pine at the height preferred.
>
> The coal tit strongly preferred spruce, feeding particularly on the twigs and needles...it was rather less social than the other tits.
>
> The crested tit and the willow tit fed at all heights and showed no preference for pine or spruce. In flocks dominated by great tits they kept low, but when by themselves they were seen feeding at all heights.
>
> The marsh tit showed a preference for feeding low down, especially in small trees. It preferred deciduous trees where they were available.

Snow observed the great tit to feed more frequently on the ground than any other titmouse species. Similarities to feeding habits in England are striking—ground feeding in great tits, high-level foraging in blue tits, the activities of coal tits in seeking among the needles of conifers, the preference of marsh tits for low levels.

Table 12. *Comparison of height distributions of feeding titmice in Wytham Great Wood and at Brightwell, 1947–50*

	Blue tit	Great tit
Number of months compared	22	16
Number of months with a difference in height distribution	17	10
Number of months with a higher proportion of Brightwell birds at or above 20 ft.	0	3
Number of months with a lower proportion of Brightwell birds at or above 20 ft.	17	7

Colquhoun & Morley (1943) surveyed the vertical zonation of twelve species of bird, including five titmice, in Bagley Wood in the winter of 1941–42. They arranged the titmice in the descending order blue tit, long-tailed tit, coal tit, marsh tit, great tit: but their records were not confined to feeding birds (only 56% of the great tits observed were feeding), and the observations of seven months were massed in a single calculation for each species. Their results are scarcely comparable with those above set forth in a degree which justifies detailed discussion.

The effect of the presence or absence of one species upon the feeding habits of another, such as that described by Snow (1949) in Sweden, is not easy to establish. Variations in the dispersals of the feeding birds may be seen in communities of different composition, but the casual connexion can only be assumed. When the feeding habits of the blue and great tits of Wytham Great Wood are compared with those of the Brightwell birds, the height distributions of the blue tits are seen to differ consistently in the two areas, whereas there is little consistent difference between the habits of the great tits (Table 12). Marsh tits were very rarely seen in Brightwell, and in that area blue tits fed notably more in the lower levels than they did in the Great Wood. Such differences in distribution are at least amenable to the explanation that in the Wytham woods blue tits were excluded from the lower levels by the pressure

of competition with marsh tits. But a second possible explanation must be noticed. In the village many people feed wild birds at bird tables, and the blue tits may have acquired the habit of seeking food at unusually low levels. Snow (1952) found that in arctic Lapland great tits are entirely dependent on human habitations for their livelihood.

It may be advanced that no proof has been given of the immediate ecological relevance of the differences of routine observed. The feeding habits as now seen may have had survival value in times past but may bear no present relation to the food supplies and requirements of the titmice. Were the feeding habits of each species fixed and unvarying, as for example are general patterns of song, this objection would be a serious one. But it has been shown that the feeding habits of the titmice are variable from season to season and from place to place, and that in the majority of cases a variation in feeding behaviour can be correlated with a variation in food supply. The upward movements of great tits and marsh tits at the time of appearance of the summer caterpillar harvest; the hunting in beeches in the good mast year of 1948 (Table 13); the effect of the Brightwell walnut harvest of 1948 on the blue tits of that village may be cited as striking examples of the adaptability of foraging behaviour.

Table 13. *Records of feeding in beeches (expressed as percentages of total numbers of trees visited) in Wytham Great Wood in October and November*

	Great tit	Blue tit	Coal tit	Marsh tit
1947	0	0·6	0	2·54
1948	19	6·3	4·2	8·7
1949	0	0	0	0

It has been shown that when, as in the early months of summer and in autumn, ecological separations between two or more species have disappeared there has been available in that period a temporarily superabundant supply of food. With the ending of that abundance the different species have returned, each after its kind, to the accustomed and separate foraging places. Were suitable foods always to be found in superabundant measure, the evolutionary significance of the segregation of the different species for so large a part of the year (and the temporary disappearance of these segregations) would be difficult to explain. But the regular appearance of separating mechanisms as soon as patently rich supplies of food are exhausted urges that pressure upon food stocks 'which gives the ultimate limit to which any species can increase' (Darwin 1859) is such that the force of intra- and interspecific competition working in combination must be avoided.

The influence of food supply upon the populations of the different species of titmice has not been proven. But the foraging habits here described are such that their survival value may be traced to the partial separation of each species from the others and the resulting diminution of interspecific competition. Only by the evolution of specialization of feeding habits are several closely allied species able to occupy and to exploit a single habitat. These specializations the English titmice show.

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It is a pleasure to express my gratitude to my colleague, Mr D. W. Snow. During some 18 months, and especially in the winter of 1947–48, he provided me with figures on feeding behaviour which made most valuable additions to my own data, and have contributed materially to the conclusions here discussed. I have had the good fortune to be able to discuss this work, at all its stages, with Dr David Lack, F.R.S., to whom I am grateful for his liberality of both time and thought.

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SUMMARY

1. The feeding habits of five species of titmouse in an area in the English Midlands have been observed over a period of three years.

2. It is shown that each species of titmouse has a characteristic height distribution of foraging activities, and preferences for certain species of trees and parts of trees. The height distribution of some species varies from season to season, and may be modified by an unusual abundance or lack of some food.

3. It is shown that the height-frequency distribution of the foraging activities of each species, and also the favoured feeding tree, differ from those of the other four species.

4. From time to time the ecological separations between different species have been found to disappear. It has been possible to show that these extinctions of ecological separation have coincided with temporary superabundances of food.

5. The ecological implications of the differences in feeding habits are discussed.

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PLANKTON PRODUCTION IN SCORESBY SOUND, EAST GREENLAND

By P. S. B. DIGBY, M.A.

*Department of Zoology and Comparative Anatomy, University of Oxford**

(With Plate 4 and 5 Figures in the Text)

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INTRODUCTION

There is no information readily available concerning the quantities of plankton, in exact terms, developed over the year in the cold waters close to the edge of the ice in the arctic regions of the North Atlantic. In order to make accurate comparison between the plankton of two regions which differ in the seasonal pattern of abundance, it is necessary to make observations over a period of a year in each, with nets equipped with meters to record the amount of water which passes through them.

This paper describes such a series of truly quantitative measurements of phytoplankton and zooplankton at Scoresby Sound, East Greenland, and comparison is made between the abundance of the plankton at this locality and the better known area of the English Channel (Harvey, Cooper, Lebour & Russell 1935; Harvey 1950). A description is given of the phytoplankton succession, not hitherto fully described over a whole season in East Greenland waters.

* Now at Department of Biology, St Thomas's Hospital Medical School, London.

The population developed is dependent, in the first instance, on the phytoplankton. The growth of phytoplankton was found by Nansen (1902) to be very slight under the ice, but to set in when it melted. This onset of phytoplankton growth during the melt in northern waters was further shown by the work of Ostenfeld & Paulsen (1911) on the plankton collected by the 'Danmark' expedition in north-east Greenland, by the work of Sverdrup (1929) on the distribution of oxygen and pH in the shelf waters north of Siberia, and that of Kreps & Verjbinskaya (1930) in the Barents Sea, of Braarud (1935) and Nielsen (1935) in the east Greenland current, of Shirshov (1935, 1937) in north Russian waters, and of Thorson (1936) in the Franz Joseph Fiord and at Clavering Island on the east Greenland coast. Until 1937 there was no information which suggested that there was any production in the areas farther north covered by

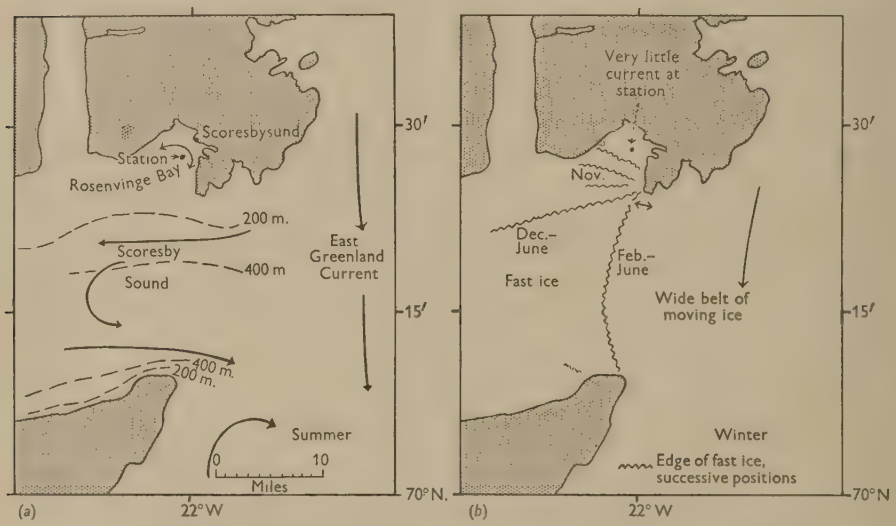

Fig. 1. Sketch maps of Scoresby Sound showing (*a*) currents in summer (partly after Koch 1945) and (*b*) currents and successive positions of fast ice in winter

continuous ice, but in that year Shirshov (1938) found a burst of diatoms and nauplii in the summer beneath the apparently continuous ice-fields north of Greenland.

The zooplankton animals feed upon the phytoplankton during the short summer, and by growth and reproduction a quantity of zooplankton is built up, and a part of this population survives the rest of the year, some 10 months, until the next season of production (Shirshov 1937; Bogorov 1938; Ussing 1938).

The observations at Scoresby Sound were nearly all made at a position in Rosenvinge Bay at lat. 70° N., long. 22° 03′ E. one or two miles offshore from the settlement of Scoresbysund, where there is a depth of about 80 m. (Fig. 1). On two occasions, when the snow was thick in winter, plankton hauls were made at a position a few hundred yards offshore where the depth was 56 m. For a description of the area see Ussing (1934). The water is, zoogeographically, probably 'high arctic' (Madsen 1936), and the open season is restricted to little more than two months.

Sampling through a hole in continuous ice-cover blown with explosive some days previously—the method used in February and March.

APPARATUS AND METHODS

In the open season samples were taken from a 17 ft. Norwegian rowboat driven by a 'Seagull' clutch model outboard motor, and fitted with a hand winch and meter-wheel. During the rest of the year, that is from mid-October 1950 until the end of June 1951, they were taken through holes in the ice, chipped or blown with explosive. When the ice was weak, at the beginning of its formation and towards the end of the melt, the nets were worked from shark line by hand, and for the rest of the time the winch and meter-wheel were mounted on a light dog sledge. Scoresby Sound enjoys a comparatively mild climate for the arctic, and no hut was used over the hole, all samples being taken in the open (Pl. 4). Metal parts of the equipment likely to come in contact with the unprotected hand were bound with insulating tape to prevent frost-bite and also to render them less slippery when iced, and certain other modifications were made, such as the use of snap-hooks instead of shackles, and the substitution of waxed sashcord in place of rope on the nets. A bucket of sea water heated on a primus stove was used to prevent water sample bottles from freezing and to thaw the water-bottle tap in the coldest weather.

A Pettersen-Nansen insulating water-bottle was used for the observations on temperature and salinity, the water samples for salinity being stored in 2 oz. bottles with rubber bungs and titrated in England by the Government Chemist. A 20 cm. Secchi disk was used for transparency measurements, worked either from the wire or from a length of shark line.

Water for assessment of total plant pigment was taken by water-bottle from each of the depths, 1, 10, 20, 30, 40 and 50 m., 500 ml. from each depth being mixed together in a large glass bottle having a capacity of about 3·5 l. On return to the laboratory between 1 and 2 l. were passed through a membrane filter of 0·62μ average pore diameter by suction from an aspirator equivalent to a head of about 2 ft of water. The pigment from the filtrate was extracted with 1–2 ml. of acetone and compared with a standard without further concentration.

In order that the summer and winter hauls should be strictly comparable, the quantitative work was based on vertical hauls with nets equipped with meters (Fig. 2). The fine net used for the phytoplankton and small copepods was a modified Apstein net of 200 meshes/in., and the coarse net was a townet, 50 cm. diameter at the mouth, 2 m. long and 48·5 meshes/in. Two calibrated Clarke-Bumpus type plankton samplers (Clarke & Bumpus 1940) had been taken, each fitted with a meter similar to the type used in the Harvey net (Harvey 1934) and the meter from one of them was fitted in Greenland into a lighter barrel similar to that of the plankton sampler. Tests in which the one meter in its new cylinder and the other meter in its original housing in its sampler were run side by side showed the proportions between the readings of the two to remain unaltered, indicating that the calibration had not been changed by transferring the first meter to its new housing. The meter in the cylinder was fastened to a frame by which it could be clipped into position in each net. In the fine net the original brass rim of the Apstein net was removed and the cylinder containing the meter was lashed directly to the canvas of the constricted mouth, the volume of water which passed through the net being indicated directly by the meter. The filtering area

of the netting was considerably greater than in the Harvey net of the usual dimensions. In the medium net, the same meter was fixed across the mouth and the amount of water which passed through the net was taken as the amount through the meter multiplied by the ratio of the area of the mouth of the net to the area of the mouth of the meter cylinder. That this assumption is not too greatly in error in shown by the general agreement between the weights per cubic metre of the medium-sized copepods calculated from the catch of each net (Table 4). Both nets were rigged so as to fish on both the ascent and descent, and to turn round at the bottom without losing the catch. The fine net was fished vertically with a 7 lb. lead on the wire, from surface to 50 m., and to the surface again one or more times, up to ten, according to the density of plankton. In winter, a first set of hauls was preserved in formalin, and a second

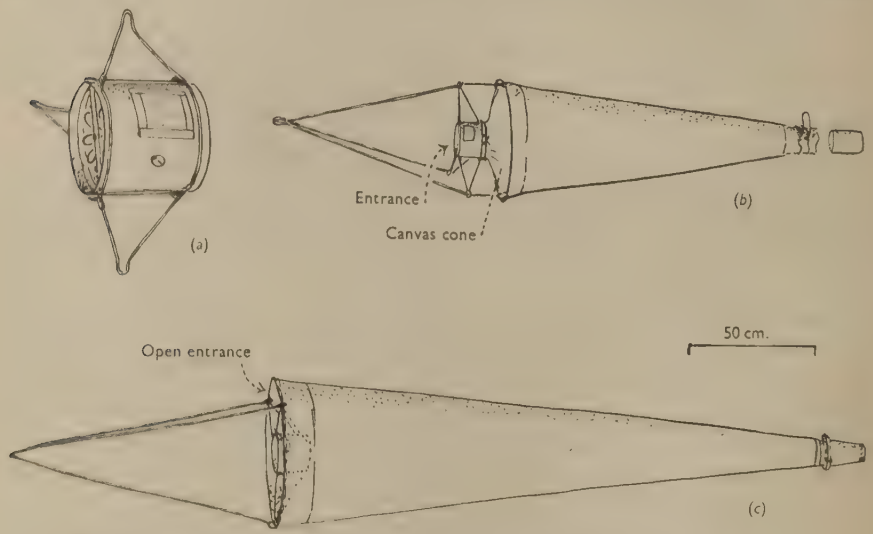

Fig. 2. (*a*) Water-meter in barrel; (*b*) meter fitted to modified Apstein net; (*c*) meter fitted in mouth of coarse townet.

similar set was taken for pigment assessment, while in summer the catch from all fine net hauls were mixed together and a proportion removed for pigment. The meter was then transferred to the medium net and this was fished in the same manner, except that as a rule two 7 lb. leads were used. The speed of passage of nets through the water was roughly 1·5 m./sec. when running out and 0·75 m. sec. when hauling in. The fine net commonly filtered 0·75 m.^{3} of water in one 0–50–0 vertical haul, the medium net 10 m.^{3}. The volumes of water fished in two to ten hauls therefore ranged from 1·5 to 7·5 m.^{3} for the fine net and 20–100 m.^{3} for the medium net; they are given in Table 2. The amount fished as calculated from the flow through the meter came to roughly one-half the water in the path of the net in each case. For comparison it might be mentioned that the plankton sampler, towed behind the boat in the open season at a speed of about 3 m.p.h., was found to filter one-quarter of the water in the path when fitted with a net of 50 meshes/in. and one-tenth with a net of 200 meshes/in.

The catches of the fine and coarse mesh nets were considered together in assessing the biomass of different groups and the numbers of different organisms. Large organisms other than copepods were picked out and the copepod fraction of the sample was rinsed through small seives of silk mesh of 27 and 48·5 meshes in. to give coarse, medium and fine fractions as follows:

Coarse fraction (material held on 27 mesh sieve): *Calanus hyperboreus*; *C. finmarchicus*, stages IV, V, VI; *Metridia longa*, stages IV, V, VI.

Medium fraction (material held on 48·5 mesh sieve): *Calanus*, stages I–III and nauplii; *Metridia*, stages I–III; *Pseudocalanus*, stages II–VI; *Microcalanus*, some stage VI; *Oithona*, stages IV, V, VI.

Fine fraction (material passed through 48·5 mesh sieve): phytoplankton, detritus, tintinnids, etc.; copepod eggs and nauplii; *Pseudocalanus*, stage I; *Oithona*, stages I–III; *Microcalanus*, stages I–V; *Oncaea*, stages I–VI.

Each fraction was weighed after rinsing on to a small disk of silk, and removing excess water by touching the under side of the silk with filter-paper. In the coarse-net samples, organisms other than copepods were separated into groups and the copepods were treated as before, except that there was no 'fine' material. The medium fraction of the coarse material did not correspond exactly to the medium fraction of the fine-net material, for the medium-meshed sieve used in the laboratory holds back some species and stages, notably *Oithona* adults, which it allows to slip through when used as a net in the sea.

Phytoplankton counts were made on a quantity of the fine fraction equivalent to between 50 ml. and 500 l. of water, arrived at by diluting the fine fraction to the appropriate amount in one or two stages as necessary, removing 1–10 ml. from the last dilution with a wide-mouthed pipette, centrifuging and examining on a microscope slide ruled in 0·1 in. squares.

PHYSICAL CONDITIONS

(*a*) *Hydrography and ice cover*

The general hydrography of Scoresby Sound for 1891–92 was described by Ryder (1895). His observations included a series taken at intervals through the year at a position off Danmarks Island, up towards the head of the fiord. He found (see also Ussing 1934):

(1) A fiord water layer from surface to 20–40 m. with temperatures above 0° C. and low salinity, formed afresh each year.

(2) A layer of polar current water from the surface or 40 m. to 400 m. with temperatures below 0° C. and salinities of 32·30–34·80‰.

(3) A warm layer with temperatures above 0°C. and salinities from 34·69 to 34·95‰.

He found the coldest water to be at about 100 m. throughout the year, suggesting that it was derived from the open coast and not formed *in situ*. He found the temperature of the warm bottom layer to decrease in winter and suggested (see Ussing 1934) that there is an inward flow of underlying water in summer developed as a counter current to the fresh (fiord) water run-off, and that this inward-flowing more saline water slowly mixes during winter with the cold-water layer.

Further observations were made in Scoresby Sound in the summer of 1932 by the Danish East Greenland Expedition (Ussing 1934), and conditions were found to agree essentially with the above and with those described for the Franz Joseph Fiord by Spärck (1933), apart from the surface layer of fiord water in summer not being so thick in Scoresby Sound in 1932 as in the Franz Joseph Fiord. This latter is to be expected as the ice from the East Greenland current drifts into Scoresby Sound and is commonly much more prevalent there in summer than in the Franz Joseph Fiord. Ussing found the cold polar current layer to thin out towards the head of the fiord, as noticed by Spärck for Franz Joseph Fiord.

At the end of August 1950 new ice crystals were already forming on the surface of the water in Rosenvinge Bay. From then until the middle of October the ice formed and reformed as thin sheets and pancakes, and this new ice together with masses of the old Polar floes drifted back and forth, sometimes packing tightly and almost completely covering the surface, and sometimes open or drifted away for a mile or two, leaving a water surface which rapidly thickened with new crystals. The sludge of crystals in Rosenvinge Bay consolidated to form sheets of fast ice in the middle of October and reached a thickness of about a foot, but blew out in a blizzard and reformed in the middle of November. The temperatures in the upper 50 m. (Fig. 3) were almost uniform at about $-1°$ C. at the end of September, and salinities ranged from 29·00 ‰ at the surface to 32·00 ‰ at 50 m. With the formation of ice the water became colder reaching $-1·7°$ C. at all depths and a salinity of 32·00–32·50‰ by November. From the middle of November until March little further reduction occurred, temperatures ranging from $-1·70$ to $-1·80°$ C. A slight increase in salinity occurred over the period as the ice-sheets grew thicker, and at a position a mile offshore in Rosenvinge Bay they had by mid-March reached a maximum thickness of about 5 ft., covered by a foot or more of hard packed snow. Three or four miles out in the Sound, where the heavy floes of Polar ice had become frozen in, deep drifts of snow formed in the lee of the hummocks, and the average total thickness was of course considerably greater. From November onwards the fast ice, which first of all occupied an area of a few miles in the bay, increased by the freezing in of more sheets to the seaward edge, and by March the limit of the fast ice followed a line directly across the mouth of the Sound from Cap Tobin to Cap Brewster. The extent of the fast ice was continually being enlarged at the seaward edge by the freezing in of new pans of ice which would then break up and carry away in windy weather. Out on the open coast the water was sometimes covered with ice as far as the eye could see, and occasionally following a wind, clear and open. From April onwards a rise in the temperature and a decrease in the salinity occurred. This may at first have been the effect either of the bright sunshine on the water outside the area covered by fast ice or by drainage from the land. There is no fixed date for the beginning of the melt, as melting begins in the heat of the sun with air temperatures below 0°C. The air temperatures in early April were well below 0° C., but after mid-April, the dark rocks became heated by the sun, and melt water filtered down beneath the snow cover. In many places on the lower slopes of the hills from mid-April onwards a snow morass developed, the water welling up to the surface and freezing at once in the cold air. Much of this water undoubtedly filtered down through the gravel and porous rocks, and passed directly beneath the

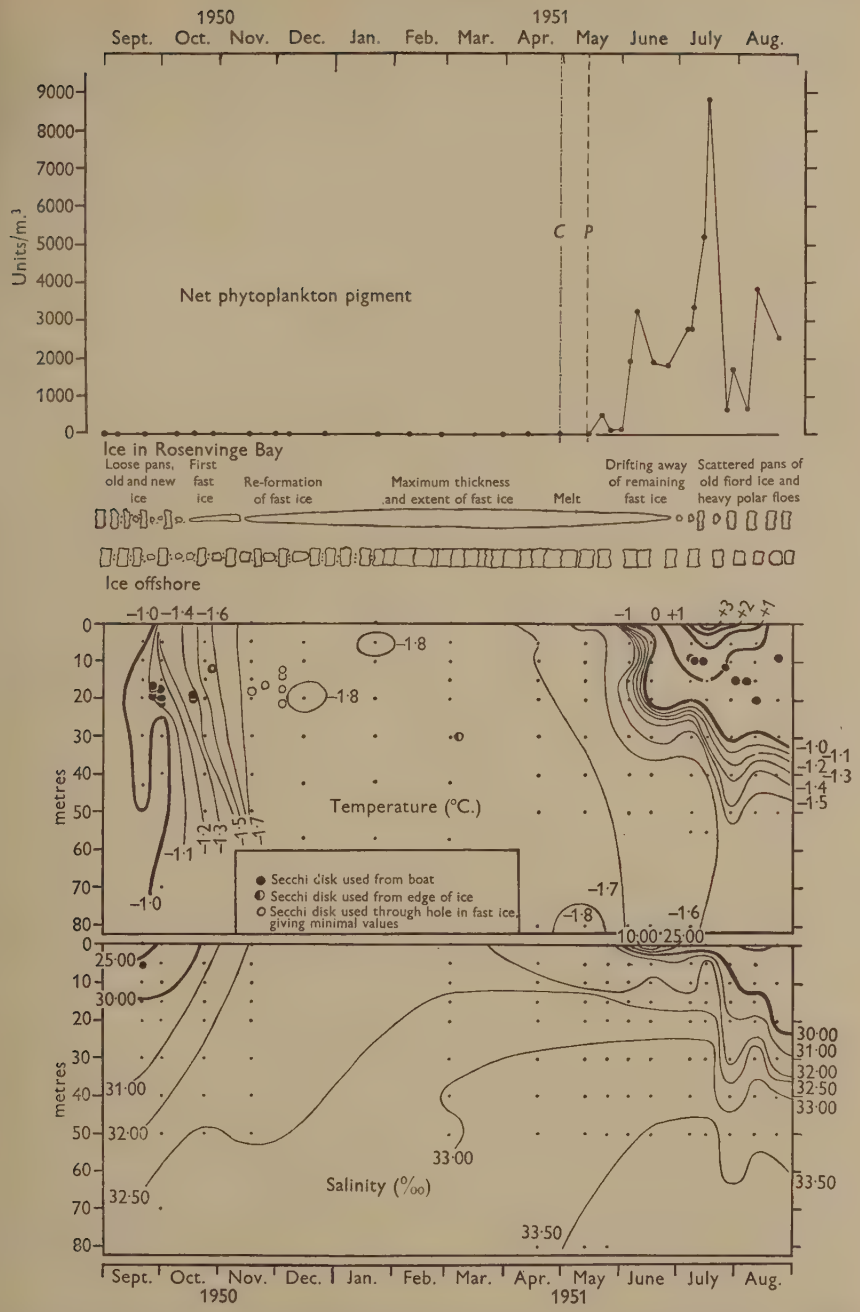
1950
1951
Sept. Oct. Nov. Dec. Jan. Feb. Mar. Apr. May June July Aug.
Units/m.³
Net phytoplankton pigment
C P
Ice in Rosenvinge Bay
Loose pans, old and new ice
First fast ice
Re-formation of fast ice
Maximum thickness and extent of fast ice
Melt
Drifting away of remaining fast ice
Scattered pans of old fiord ice and heavy polar floes
Ice offshore
Temperature (°C.)
Secchi disk used from boat
Secchi disk used from edge of ice
Secchi disk used through hole in fast ice, giving minimal values
Salinity (‰)
metres

Fig. 3. Phytoplankton, ice and hydrography in the upper 50 m. at Scoresby Sound in 1950–51. *C*, date of onset of spring phytoplankton growth as seen in cell counts; *P*, date by which growth of phytoplankton was sufficiently advanced to show as an increase in net pigment.

ice and into the sea. This is suggested also by the observation that the water below the hole which was kept open a mile offshore became distinctly turbid and of slightly reduced salinity in mid-April, although there was no obvious melt in progress. Streams on land did not begin to run as such until the beginning of June. During April, May and June the area of fast ice grew less by the breaking off of large floes, first of all from the area of fast ice in the centre of the Sound, and then from the edges of the remaining sheets, the detached sheets joining the general stream of ice and being carried out to sea and southwards by the current. The rise of water temperature and decrease of salinity was very slow until the beginning of June, when the fast ice was melting rapidly and the open water offshore was increasing in extent. During June sheets of melt water formed on the ice, and late in the month found their way down through holes and cracks. Towards the end of June the remaining sheets of fast ice became completely melted for 200 yards or so offshore from the settlement, off the mouths of the streams and at various places joining the land, where the dark rocks on shore hastened the melting of the ice by radiation. Offshore the sheets were broken up into hummocks, ponds and drainage channels with grey translucent bottoms and occasional holes through which water drained away. These rotten sheets, held in place largely by several grounded bergs, finally fragmented and started to drift out in a squall at the end of June. The melt is characterized by a progressive reduction in the total area of the ice-cover as much as by the thinning down of the individual sheets. Throughout July and August in 1951 there were always masses of drifting ice in the vicinity; fragments of old fast ice, heavy polar floes from the East Greenland current and bergs derived from the big glaciers at the head of the fiord. The water temperature reached a maximum of 3·0° C. at 1 m. in July, and the 0° C. isotherm reached a maximum depth of between 15 and 20 m. at the end of August. The salinities dropped to 10·00‰ at a depth of 1 m. through the ice in June, but the surface layer of brackish water was thin and the salinities at 10 m. did not drop below 30·00‰ until August, when cooling at the surface had set in. The temperatures on 23 August were −1·0° C. at the surface and at 10 m., and this, together with the thickness of the sheets of new ice forming on the surface in the first few days of September, gave the appearance of winter setting in some 3 weeks earlier than in the previous year. This effect was probably partly due to the moving down the coast and into Scoresby Sound in August of very heavy and closely packed masses of polar ice of unusual extent, together with their associated layer of cold surface water.

During the formation of the fiord water the stability of the surface layers is very great by reason of the reduction in salinity, and it can be seen from Fig. 3 that the warm wave travelled downwards by turbulence at the rate of about 12 or 13 m. month during June, July and August, while the cold wave during the period of overturn from August onwards passed downwards at about 50 m. month. The speed of downward passage of the peak of temperature in this present series appeared to be about 20 m. month in the top 40 m. in July and August. This lag can be seen in Ryder's series of curves (1895, p. 211) where his August peak temperature at the surface can be seen to occur later with depth, being at 10 fathoms in September, at 15 fathoms in October, at 25 fathoms in December and apparently at about 50 fathoms in February, when it is scarcely distinguishable. This represents a rate of downward movement of the peak at a little under 20 m./month.

Ussing has pointed out the similarity in density between the Polar Current water and the underlying warmer layer with consequent lack of stability. The slow admixture of the more saline lower layers with the upper 50 m. is shown by the gradual increase in salinity from summer onwards, freezing out of the ice being responsible for little of the increase in salinity at 50 m. As the salinity of the water at 50 m. increases through the year by admixture with more saline water from below until it is lowered by admixture of fresh water from the fiord water layer above which mixes but slowly, the maximum salinity at 50 m. occurs in summer at the time of maximum temperature of the surface water.

(*b*) *Movements of water and ice*

Water movements in the fiords have been considered by Ryder (1895), Spärck (1933), Ussing (1934, 1938) and Koch (1945). Koch has dealt in great detail with water and ice movements on the coast. Throughout the year there is a general movement of the east Greenland current down the coast at a very variable speed, estimated by the 'Arctic Pilot' to be 4 miles/day just off the coast and 15 miles/day east of Jan Mayen. Water and ice from this current flow in on the north side of the entrance to Scoresby Sound and out again on the south side. Superimposed on this there is in the fiords in summer a general outward movement of fresh water run-off at the surface and a compensating inward movement of the lower layers. There is in summer a vigorous eddy movement in Rosenvinge Bay, but in winter when fast ice covered much of the sound very little movement of the water occurred at the station, although a powerful tidal current ran in and out of the fiord off Cap Tobin, some 3 miles away. It is not possible to be more precise than to say that the water in Rosenvinge Bay represents an eddy of the main stream subject to more rapid renewal from the East Greenland Current in summer and less rapid renewal in winter.

(*c*) *Transparency*

From the end of September until the middle of November the depth at which the 20 cm. Secchi disk disappeared was 18–20 m. The first observations were made by boat; the mid-November observation was made through a small hole in the new sheets of ice not yet covered by snow or hoar frost. Subsequent observations through the ice when covered with snow represent not true but minimum values. When the ice-cover became too thick, no further observations were made until 10 March when a visit was paid to the edge of the ice where a large floe of fast ice a mile south of Cap Tobin had broken off and drifted away, leaving for a short while an area of open water. The Secchi disk was lowered into the water and observed from the edge of the ice. The sun in the south, partly obscured by banks of mist, illuminated the disk, the fast ice being to the north of the open water. The disk was visible to 30 m., and the water was noted to be of a very clear deep blue colour. No further measurements were made until after the melt, when a number of observations were carried out from the boat in July and August, giving values increasing from 10 m. in early July to 20 m. in mid-August, with a final value of 5 m. on 23 August in the turbid water between the packed masses of heavy polar floes which had moved into the Sound a few days earlier.

Spärck (1933) found the water in the inner ramifications of the fiords to be on occasion very turbid with transparencies as low as 0·5–1·0 m., while the east Greenland current proper had values of 13–16 m. Thorson (1936) found the water at Ella Island to be clear in June but more turbid towards the end of summer. In this series of observations in Scoresby Sound the transparency appears to be directly related to the amount of melting, being great in winter and therefore at the beginning of the phytoplankton growth, and most turbid at the break up of the ice, then increasingly clear during July and August, apart from the anomalous figure in the leads between the floes at the end of August.

(*d*) *Illumination*

Since the latitude of Scoresby Sound is 70° N., the sun stays below the horizon for a short while in winter and is above the horizon at night for a short while in summer. Owing to the clear atmospheric conditions it shines brightly in the early months of the year in Rosenvinge Bay, but June and especially July and August have some cloudy and foggy days. Out at sea and in the centre of the Sound a few miles from the settlement there are often dense banks of fog in July and August, while the inner reaches of the Sound are clear. Illumination conditions in Rosenvinge Bay are therefore more favourable for the growth of phytoplankton than are those of the east Greenland current itself with its banks of fog, but less so than the inner reaches of the fiords where the ice melts earlier and there is little fog.

PHYTOPLANKTON

(*a*) *Net-caught pigment*

Assessments for phytoplankton pigment were made on net catches throughout the year (Tables 2 and 4; Figs. 3 and 4). At the beginning of September 1950 the net pigment was present at a value of less than 10 units/m.^{3}. From September 1950 until the end of April 1951 the pigment values in the waters beneath the ice were less than 1 unit/m.^{3} as estimated from up to 3 m.^{3} of water. The pigment did not appear to be so scarce as might be implied from the cell counts, usually about 0·3 unit was found. Possibly some of this was from detritus of plant origin. The pigment increase at the hole in the ice was not detectable until 12 May when the surface of the water by the hole was still covered with 3 ft. or so of fast ice, although there was open water offshore. The first new diatoms had been found in the counts of 29 April. This occurrence of new diatoms beneath the fast ice has been noticed before in Greenland by Vanhöffen (1897), but the presence of diatoms at the hole early in the year is not evidence that sufficient light penetrates the 3 ft. or so of ice as they may have been brought in by water movements from open water some distance away. The increase beneath the ice was slow, but the values rose rapidly immediately after the melting and moving out of the remaining fast ice at the end of June. The main peak with values of up to 9000 units m.^{3} occurred between the beginning of June and mid-July. Following a decrease at the end of July and early August there was an increase again in late August. When the last samples were taken, on 23 August, a heavy field of ice had moved in and there was still a density of 2570 units/m.^{3}. The average for the three months of June, July and August was 2929 units/m.^{3}, while the yearly average density

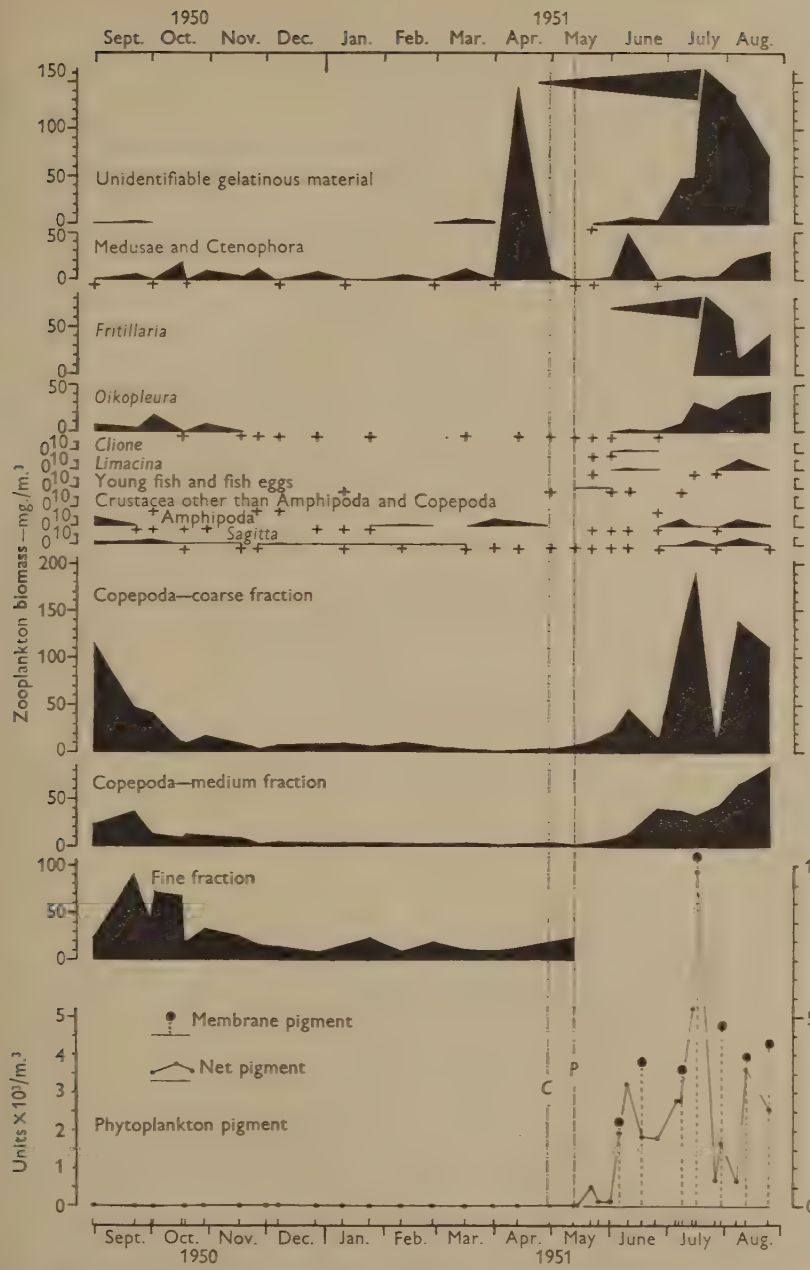

Fig. 4. Biomass of zooplankton organisms, and net and membrane phytoplankton pigment in upper 50 m. at Scoresby Sound in 1950–51. –, present but < 1 mg. m.³. *C*, appearance of the first new diatoms of the year in the cell counts. *P*, onset of the spring production as seen in pigment values.

of net pigment, supposing it to be based on weekly observations spread over the whole year, would be 670 units/m.^{3}.

(*b*) *Membrane pigment*

Assessments for membrane pigment were made during the summer of 1951. The seven values of membrane pigment ranged from about equal to, to three times as much as, the net pigment, and the average for June, July and August was 4557 units as compared with 2929 units of net pigment for the same period. The membrane pigment gave the appearance of being relatively more abundant as the season advanced. As noted by Harvey (1950), the membrane pigment was more yellow than the net-caught pigment. No membrane pigment assessments were made in September 1950, but examination of a $\times 50$ membrane filter concentrate of mixed water samples from all depths on 21 September, 1 October and 18 November revealed no obvious flagellates, although there were occasional non-motile spherical bodies which may have been of plant origin. A few water samples were examined for flagellates later in winter, but there appeared to be virtually none. The biomass and sizes of copepods caught by the coarse net showed a sharp decline in September, suggesting that the nannoplankton organisms which were lost by the net had, if they were available to copepods and were present in great abundance, a similar period of abundance to that of the net-caught phytoplankton. The proportion of net to membrane, that is, to total pigment at Scoresby Sound, was perhaps remarkable in that the net caught so much of the total; the comparison made by Harvey (1950) indicated that in the English Channel the net took only a small part of the total pigment.

(*c*) *Abundance and species composition at Scoresby Sound*

The succession of species in the phytoplankton associations is shown in Table 5. The specific names of the diatoms are those accepted by Lebour (1930). From the end of August 1950, throughout winter until the beginning of April 1951, the population consisted of several species of *Chaetoceros*: *decipiens* (the most abundant), *convolutus*, *concavicornis*, *subtilis*, *debilis*, *teres*, *densus*, *atlanticus*, *borealis*, and a few specimens that appeared to be *C. gracilis*. They were accompanied by occasional *Coscinodiscus* (a species close to *subtilis*), *Rizosolenia* (mainly *styliformis*) and *Fragilaria oceanica*. *Ceratium arcticum* and other thecate peridinians were present throughout winter, the former by reason of its large size being by far the most conspicuous member of the winter phytoplankton. The total number in terms of cells per litre was very low, declining from the order of 10 to 100 in September to 0·5 in March and April. As these were net hauls, small thecate peridinians were no doubt considerably more abundant than the figures suggest. The catches of 12 April contained only these forms, but on 29 April there was evidence of the beginning of the spring increase in the appearance of an association of *Nitzschia frigida*, *Amphiprora hyperborea*, *Navicula septentrionalis*, *N. grani*, *N. pelagica*, *Fragilaria oceanica*, *Thalassiosira nordenschioldii* and *T. gravida*. The chains were at first short, and the numbers were still too low to show an increase in the pigment assessment until the next sampling day, 12 May. *Amphiprora* and the species of *Navicula* were more abundant at the beginning of the outburst, beneath the fast ice during May and in the open water during June, but they

were also abundant again at the middle and end of July, when the fiord was on occasion packed with drift ice. *Phaeocystis* was common throughout the summer, independently of the succession as noted by Braarud (1935) in the polar waters of the Denmark Strait. Species of *Chaetoceros*, mainly *debilis* and *decipiens*, became abundant in July, and continued through until the end of August, when they were dominant in the last samples taken, in which *Thalassiosira* and *Fragilaria* had disappeared. Peridinians became abundant in July and August at the same time as the tintinnids. The association of *Chaetoceros* species, *Ceratium arcticum* and other thecate peridinians, together with tintinnids at the end of August, was the same as that met with the previous September and throughout the winter. Of the tintinnids, *Ptychocylis obtusa* Brandt and species of *Cyttarocylis* were the most common, while *Tintinnus secatus* Brandt, *T. pellucidus* Meunier, *T. gracilis* Brandt, *T. vitreus* Brandt and one or more species of *Tintinnopsis* rather similar to *nitida* Brandt occurred spasmodically.

There was thus a succession closely similar to that found by Shirshov (1938) in north Russian waters, of an early 'spring' phase of *Nitzschia*, *Fragilaria*, *Navicula* and *Thalassiosira* and a late 'summer' phase of *Chaetoceros*, *Ceratium* and other peridinians and tintinnids, continuing through the winter in diminishing numbers until the following spring. In the early phase *Nitzschia* and the species of *Navicula* and *Amphiprora* were closely associated with the presence of thick ice.

(*d*) *Previous observations on the species succession in the East Greenland current and in north Russian waters*

Cleve (1900), working on the collections of the Swedish Expedition of 1899 to East Greenland, found drift-ice samples to be characterized by *Chaetoceros* spp., *Coscinodiscus*, *Fragilaria*, and *Thalassiosira*, and the fiord samples to be poor, with *Chaetoceros decipiens*, *Ceratium arcticum* and *Cyttarocylis* with quantities of copepods. The drift-ice samples were similar to the later part of our early phase and the fiord samples were late phase, which is in good accord because the fiords are clear of ice at a comparatively early date, and the plankton production can set in earlier than on the coast, where the ice and fog restrict the amount of light available. Broch (see Damas & Koefoed 1909) found an association similar to the early phase at Scoresby Sound in samples taken in the drift ice and coastal waters of East Greenland in 1905 by the Duke of Orleans's expedition. Ostenfeld & Paulsen (1911) described from Danmarks Havn a population corresponding to our early phase in August; the open season there was shorter than at Scoresby Sound in 1950–51, and the production only began in late June. Late-phase plankton, *Ceratium*, species of *Chaetoceros*, tintinnids and peridinians, were taken in October. Plankton taken in the drift ice on that expedition appears to correspond to our late phase.

Steeman Nielsen, reporting on plankton samples taken by Madsen at Clavering Island in 1932–33 (Thorson 1936), found the population to be rich in August 1932 with species of *Chaetoceros*, to decline in September and October, and to begin next June with *Nitzschia frigida* and continue with *Fragilaria oceanica* and *Nitzschia seriata*. This again was essentially the same succession as at Scoresby Sound. He attributed the rich samples of August to the rising to the surface of a deeper-lying water-layer rich in nutrients as an exceptional phenomenon. As these Scoresby Sound samples

show the same rise, although the growth might well be due to the presence of nutrient-rich water previously under ice, it may also well be due to the bringing to the surface of nutrients by the beginning of overturn, for the surface cools progressively from mid-July onwards. If this is the case, the late August peak may be a normal feature equivalent to the autumn peak in more southern waters, still separable from the spring peak although the open season is so short.

Braarud (1935) found that in centrifuge samples the succession in polar water in the Denmark Strait was initiated by flagellates and continued by an *Achnanthes-Fragilaria*, a *Thalassiosira-* or *Chaetoceros*-vegetation to a scanty *Detonula*-vegetation with dinoflagellates. Nielsen (1935) found a population corresponding to our early phase in the East Greenland current in early summer and a population of peridinians, flagellates and *Chaetoceros decipiens* later in summer when the nutrients were exhausted. Shirshov (1937) found in collections made in north Russian waters in 1932–35 a succession beginning with *Thalassiosira gravida*, *Fragilaria oceanica*, *Achnanthes taeniata* and *Detonula confervacea*, which he called 'spring' species, followed by 'late spring' species, *Chaetoceros socialis* and *furcellatus* and 'summer' species *C. debilis*, *compressus*, *diadema*, *mitra* and *teres*, together with peridinians which became more predominant as the season progressed. Such a succession did not appear to be clear in the samples taken farther north where the ice cover is more continuous, that is in those taken from the *Sedov* in the ice north-east of Spitsbergen in 1937–39 (Usatschev 1946), and by Shirshov from the drifting ice floe north of Greenland in 1938 (Shirshov 1938). Nansen's samples from the *Fram* unfortunately give us no information on the summer succession.

It would appear, therefore, that the sequence of net phytoplankton found in Scoresby Sound, that is, an opening phase of *Nitzschia* and *Fragilaria*, continuing with *Thalassiosira* and *Chaetoceros* and ending with *Chaetoceros*, *Ceratium* and other peridinians and tintinnids, is of very general occurrence on the East Greenland coast as well as in North Russian waters that are comparatively open in summer, although possibly the regions that have no open water have a less clear-cut succession. As none of our membrane pigment measurements were made at the very beginning of the phytoplankton outburst, we can add little to Braarud's observation that the season began with a period of abundance of flagellates. However, the appearance of the graph of net and membrane pigment (Fig. 4) suggests that in this case net-passing flagellates did not play a large part in terms of quantity.

It is noteworthy that during winter the phytoplankton never became completely absent, as reported by Hardy, Farran, Garstang & Georgeson (1936) for the top 50 m. of one of the *Nautilus* stations from north of Spitsbergen in 1931. This suggests that the complete impoverishment of a water mass by prolonged copepod feeding in a period of no growth does not occur. It may perhaps be occasioned by some process such as sedimentation from a thin surface layer of water under calm, stable conditions, followed by piling up of the impoverished layer by wind, which is perhaps more likely to occur in open water than in coastal areas with a good deal of ice which is constantly melting to supply nutrient-rich surface water.

ZOOPLANKTON

The biomass of all organisms and groups declined from the beginning of September until the following April (Table 4, Fig. 4). The phytoplankton was of negligible bulk during winter, so the fine fraction weights refer almost wholly to zooplankton organisms and detritus, which in all cases appeared in the main to be fine particles of organic refuse. On no occasion were large quantities of sand and grit encountered, as so often is the case after rough weather off the English coast. This is doubtless due to the ice cover which damps out wave motion, and is reflected in the high transparency of the water in winter. Of the three classes of copepod material this fine material, which included fine detritus, was the largest from the period September to May, apart from the anomalous first sample which may be regarded with caution because the samples were taken by a plankton-sampler towed behind the boat and are thus perhaps not quite comparable to values obtained with vertically hauled nets. After the beginning of the phytoplankton outburst in May, the weighings of the fine fraction were discontinued.

Some medusae and ctenophores were present all the year round. *Sagitta* and other organisms represented only an insignificant part of the total biomass. The inclusion of amphipods, mainly *Themisto*, in these hauls is perhaps questionable because a certain number of these cling to the under-surface of the ice round the hole, and it is not possible to say how many were free swimming and how many were dislodged by the wash of the net. The total weight of material that could be caught with these nets was estimated to be the combined total, that is the sum of the fine fraction from the fine net, the average of the medium copepods from each net, and the large copepods and large organisms other than copepods from the coarse net. This was as a rule larger than the weights of either, as the fine material was of course lost through the meshes of the coarse net and, from comparison of the yearly averages, about half the large copepods were lost by escape from the path of the fine net.

During autumn and winter when the phytoplankton was of negligible bulk, the fine fraction material represented an average of 41% of the combined total, which declined from 189·5 mg./m.^{3} on 21 September to 21·2 mg./m.^{3} on 30 March. As the weighings of the fine fraction were discontinued after the beginning of the phytoplankton outburst in May, combined total values are not available for summer. Over the winter, the coarse net itself took catches declining from 162 mg./m.^{3} on 29 August to 11·3 mg./m.^{3} at the end of March, and increasing from then to an extended peak in July and August with an average of 391 mg./m.^{3} for the five sets of hauls in these months. Much of the material in July and August was of a gelatinous nature, *Oikopleura* and *Fritillaria*, ctenophores and a quantity of mucilaginous threads and material apparently derived from the ctenophores, as noted by Ussing (1938) for late summer. The biomass of the medium and large copepods alone taken by the medium net fell from 141 mg. at the end of August to 3·0 mg. at the end of March and rose to an average of 169·0 mg. during July and August, thus constituting a little over half the weight of the net-caught matter at that time. The yearly averages of the various categories making up the total biomass are given at the end of Table 4.

A series of five determinations of the oxygen consumption of raw zooplankton was carried out in May 1951. In each case, the zooplankton was caught in the upper 20 m.

or so of the water column with the coarse tow-net, organisms other than copepods were removed, and part of the catch was transferred to bottles of about 300 ml. capacity which were suspended about 5 m. below the surface for the duration of the experiment. Initial and final dissolved oxygen was determined by the Winkler method, and when the experiment was finished the copepods were weighed on a disk of silk after removing surplus moisture with filter-paper. The results are shown in Table 1. Exps. 1–4 were carried out at the very beginning of the period of phytoplankton abundance, before the net pigment rose above 10·8 units m.^{3}, and Exp. 5 later, between net pigment values of 541 and 117 units m.^{3}. The average value for the oxygen consumption was 101·8 ml. oxygen/kg. (wet weight)/hr.

Table 1. *Respiration-rate of zooplankton copepods*

Date	Duration of exp. (hr.)	Plankton used	Wet wt. (g.)	Oxygen (ml./l.) Initial	Final	Consumed	Oxygen consumed (ml./kg./hr.)
(1) 7–9 May 1951	52	Large + medium copepods (light bottle)	0·377	8·80	1·47	7·33	103·0
(2) 12–14 May 1951	53	Large + medium copepods (dark bottle)	0·324	8·95	2·02	6·93	111·0
(3) 12–14 May 1951	53	Large + medium copepods (light bottle)	0·315	8·95	3·36	5·59	92·0
(4) 12–14 May 1951	53	Large copepods only (light bottle)	0·139	8·95	2·75	6·20	103·0
(5) 25 May 1951	25·5	Large + medium copepods (light bottle)	0·107	7·9	6·45	1·45	100·0
						Mean	101·8

If we assume carbohydrate metabolism this figure gives us 2·4 g. carbohydrate kg. (wet weight) 'burnt' per day for respiratory purposes, which is quite close to the figure of about 0·27 for the percentage required at 0° C. which can be read from Riley, Stommel & Bumpus's fig. 16 (1949), based on data from Marshall, Nicholls & Orr (1935). If we assume an 85% water content we have a daily consumption, for respiration, of about 1·6%, in fair agreement with Harvey's estimate of 4% for *Calanus* in summer in the English Channel some ten or more degrees warmer.

DISCUSSION

(*a*) *Influence of water movements*

The picture of the phytoplankton and zooplankton changes obtained at Scoresby Sound is no doubt somewhat distorted, as throughout summer there is a tendency for water from the offshore current with more fog and ice to flow in, support a crop of phytoplankton and flow out again. The maximum zooplankton production may thus be expected to be farther south, in much the same way as the phytoplankton and zooplankton populations are separated in space in Icelandic waters (Nielsen 1935). How far this operates is not clear, for generally speaking the open season is at roughly the same time for a considerable way up the coast, so that while the earlier phytoplankton observed at Scoresby Sound had developed close at hand, the zooplankton population a little later may have developed from organisms resident in Scoresby Sound itself or may have developed from a phytoplankton outburst at about the same time some way up the coast. In the same way, it is not clear to what extent the zooplankton of May and June have been the remnant of the population left in Scoresby Sound at

the end of production the previous September, or the remnant of a population developed in the far north either close to the Pole or perhaps in the waters north of Franz Joseph Land (see maps of the drift of Papanin's party and of the various vessels beset in the ice given by Zubov 1940), Papanin's party (Papanin 1938) landed close to the North Pole in May 1937, and when they had drifted only 100 or 200 miles away from that position, Shirshov (1938) found the 'spring' flowering of diatoms to occur throughout the month of August beneath the ice, and the phytoplankton expressed in chlorophyll to attain 0·4 mg./m.^{3}. This corresponds to 455 units/m.^{3} (taking 1 unit = 0·88 μg. chlorophyll—see Riley 1938), but it appears that this may refer to the density in the top 20 m. alone; if so the figure would be rather less for a haul of a net fished from a depth of 50 m. to the surface. In the absence of more precise information it appears that the average phytoplankton for the season corresponded to between 1/100 and 1/10 of the population developed at Scoresby Sound. Shirshov unfortunately gives no quantitative account of the zooplankton. Nansen (1902) found only a very poor population under the ice, but, as Hardy *et al.* (1936) pointed out, none of his plankton samples were taken in July, August or September, and it may well be that in the waters around the *Fram* there had been quite an appreciable production during these months. Stefansson (1928) criticized his conclusions as to the poverty of life beneath the ice on the grounds that his nets were streamed from the drifting boat, and as the water and ice as a rule move at closely similar speeds very little water would be fished. Papanin's party subsequently drifted to a position off Scoresby Sound by the following February. It may well be, therefore, that the winter population in the surface layer at Scoresby Sound is derived, partly at any rate, from production in the Arctic Ocean the previous summer; while possibly the larger *Calanus* that sink to the depths in winter may remain resident in the locality.

(*b*) *Turnover in Scoresby Sound: the zooplankton copepods throughout the year*

If, in the lack of certain knowledge of the amount of interchange that goes on in Rosenvinge Bay, we assume that the populations rise and fall by changes in a self-contained body of water, we may draw certain conclusions regarding their productivity.

The yearly course of the biomass of the large-plus-medium copepods and of the pigment content of the phytoplankton, smoothed by reducing the values to the three-period running mean in each case, is shown in Fig. 5. Organisms other than copepods are omitted as owing to their smaller numbers the estimate of biomass is not so accurate. They are predators on the copepods, or filter feeders of very fine material, but they constituted at the most half the total catch and on the whole have little organic content. The running mean of the copepods declined from about 150 mg./m.^{3} at the end of August to a first low value of 10 mg./m.^{3} in November. A steady period followed until February, following which the values dropped to a minimum of 5 mg./m.^{3} at the end of March, and then increased to 150 mg./m.^{3} at the end of June. The values stayed at this level throughout July and August.

The first sharp fall was caused by the sinking to the depths of late stages of *Calanus*, and to some extent of *Pseudocalanus* also. The steady values of December and January, and the fall of February and March, give the appearance of a temporary increase in the face of a general decline in the population, centred over the end of January which is probably the darkest time in the sea. This apparent increase in biomass coincided

not only with the appearance of *Metridia*, *Microcalanus* and *Pareuchaeta*, of which the mid-winter rise has been discussed by Ussing (1938), but also with the appearance of large individuals of *Calanus* and *Pseudocalanus*, and indeed the bulk of the apparent increase was due to the occurrence of these latter. It appears that *Calanus* and *Pseudocalanus* behave to some extent as the *Metridia* group in mid-winter, in that a certain number of individuals appear at the surface and sink again. The mean size of the later stages increased at the same time as did the population, suggesting that the increases were due to vertical movements and that the larger members, being more mobile, moved upward to a greater extent than the smaller. The changes in size and in population of the copepods will be considered in more detail in a later paper.

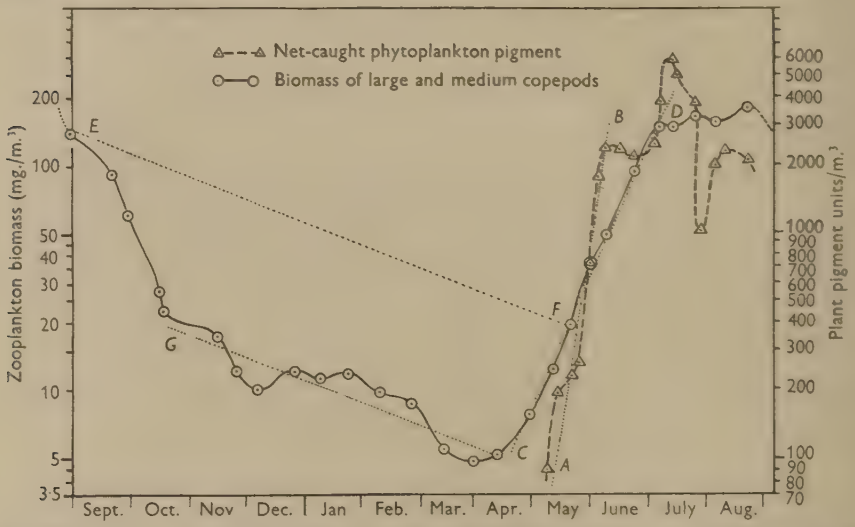

Fig. 5. Yearly course of net phytoplankton pigment and of biomass of the large plus medium copepods. All values have been smoothed by taking the three-period running mean, and plotting on logarithmic scale of quantity.

Assuming that there were no vigorous lateral movements of copepod-rich water, the beginning of the spring increase in April must be caused by upward movement, as very little phytoplankton was present, and the nauplii and youngest stages did not appear until later. At the end of the period of spring increase, the increase of zooplankton biomass was associated with vigorous growth and reproduction under conditions of abundant phytoplankton. There is no clear division line where it might be possible to say upward movement ended and growth began.

It is reasonable to suppose the true decrease in the zooplankton population over winter to be approximately exponential, the phytoplankton being of negligible bulk in the autumn of 1950. It is suggested that the rate of decline of the population between the low values at the beginning of December and at the beginning of April may represent the true rate of the decline of the population, shown by the line *GC*, although only a part of the population was present in the surface layers at this time. It is also suggested that the true rate of decline of population over winter, were the larger *Calanus* not to sink, may be represented by a line drawn from *E*, the 150 mg. m.^{3} level at the end of August before sinking set in, parallel to *GC* to meet the spring increase of

copepods *CD* at *F*, which therefore represents the point where the increase of biomass by upward movement became increase of biomass by growth. If this is so, the true decline of the population of large plus medium copepods taken in the nets in summer was from the order of 150 mg./m.^{3} at the end of August to 20 mg./m.^{3} by mid-May, or to 13·3% in eight and a half months. This represents an exponential decrease of 0·053 per day. Metabolism at the summer rate would involve a decrease at the rate of 0·016 per day, so even if the metabolic rate is the same in winter as in summer, there would be adequate material in the water to sustain the population, so long as some mechanism exists whereby the population can feed on its own members. Such a mechanism obviously exists in summer, because the reduction in numbers of a stock as it matures is so great. The growth-rate, taken from the life-history figures, showed in summer a development from Copepodite state I to VI in about three months, involving an increase in the bulk of the individual of twenty-seven times. As the total biomass appeared to increase by seven times, the discrepancy must be due to mortality. It may be that all the dead organisms sink to the bottom where they are later broken up by bacteria, but it seems quite possible that a large part, at any rate, may be returned to the population as soon as they die. Part of the food of *Calanus* is known to be of crustacean origin (Lebour 1922; Marshall 1923; Moore 1931; Lowndes 1935) and it may well be that apart from active attack on small individuals and the inclusion of nauplii in the food by the normal processes of filter feeding there may be active attack of large individuals when they are moulting. Parasites and predators all take their toll of large as well as of small individuals and leave animal matter in the surface layers in the form of particles of various sizes, which no doubt support a strong bacterial growth and are then ingested by filter-feeding forms. It may be suggested that such a mechanism can operate in the absence of phytoplankton so that the population which consists mainly of filter-feeders can support itself over a long period through reduction in its numbers by what is in effect a cannibalistic process.

(*c*) *The summer increase of phytoplankton*

On the basis of these running means, the phytoplankton showed an increase from between 100 units/m.^{3} in early May to 2400 about four weeks later, followed by a period of three months in which the values fluctuated between 1000 and 6000 units/m.^{3} with a mean of 2500. The increase of pigment from early May to early June is approximately exponential, although it is risky to draw such conclusions from samples taken at such a position, and the slope of the line drawn through the seven points covering the increase indicates a population increase at the rate of ten times in 19 days, implying a mean rate of cell division of once in about four days, which is not unreasonable. This is a minimum value because the division rate was undoubtedly lower at first, when also the grazing rate was low, and high later when the ice was melted and the area of open water larger, but when there was also a higher grazing rate because more copepods had risen from the depths.

(*d*) *Grazing-rate of the copepods*

A tentative estimate of the amount of water filtered by the copepods may be arrived at from the biomass and pigment measurements in July and August. In these two months, when the zooplankton was at its maximum, a net pigment density of 3213 units/m.^{3} supported a zooplankton population of which the copepods represented

169 mg./m.^{3}. Estimating from the oxygen consumption their requirements to be 1·6% of their body weight per day, and using assumed phosphorus content to convert zooplankton requirements to phytoplankton requirements according to Harvey's values of

1 g. wet weight zooplankton = 2·0 mg. P (Harvey 1950),
and 1000 units = 0·08 mg. P (Harvey 1934)

(from which 1 mg. wet weight zooplankton is the equivalent, on phosphorus, of 25 units of pigment), we have that the daily requirement of the 169 mg. zooplankton is 67·6 units, which was contained in 21·0 l. if net-caught pigment alone was available, of 13·0 l. if membrane pigment was available as well. The grazing-rate for maintenance was therefore 124 l./g. wet weight of copepods/day for net pigment or 77 l. for total pigment. This is in good accord, though possibly rather large, with Riley's estimate of 80–110 ml./mg. wet weight/day for the warmer waters of the George's Bank.

(*e*) *Comparison of standing crops with those of the English Channel*

It is possible to make a tentative comparison between the magnitude of the standing crop of net-caught phytoplankton pigment at Scoresby Sound and in the English Channel. Thus at Scoresby Sound in 1950–51 the year's average net pigment (supposing it to be based on roughly weekly values) was 670 units m.^{3}, while from Harvey (1934, fig. 8), the Plymouth average for 1934 was about 680 units m.^{3}, or practically the same. At Plymouth, however, it appears that a much greater part of the population consists of net-passing forms than at Scoresby Sound. We may compare the total plankton, phytoplankton plus zooplankton, using Harvey's phosphorus values for conversion and taking the year's average net pigment as 670 units m.^{3} and the year's average wet weight of zooplankton as 111·3 mg. m.^{3} as a minimum figure, that is, the total figure from the combined catches of the fine and coarse nets, but with the fine fraction zooplankton (nauplii and young stages of *Oithona* and *Microcalanus*, eggs, etc.) omitted during the summer. If these two are reduced to phosphorus content to make them directly comparable with the data available for Plymouth (Harvey 1935) using the same conversion factors as before and assuming them to hold good for material from East Greenland, the values become:

average zooplankton, $111{\cdot}3 \times 0{\cdot}02 = 0{\cdot}223$ mg. P;
average phytoplankton $0{\cdot}670 \times 0{\cdot}08 = 0{\cdot}054$ mg. P;

and the total average net-taken organic matter contains 0·28 mg. P/m.^{3}. The yearly average phosphorus in net plankton from Plymouth in 1934, taken from Harvey *et al.* (1935, fig. 11), was about 0·41 mg. On this basis, therefore, the average standing crop of net plankton in Scoresby Sound in 1950–51 was about two-thirds of that at Plymouth in 1934. As the summer nauplii have been omitted from the Scoresby Sound figures, the standing crop of the two localities may in fact be even more similar, but the Plymouth figures may perhaps be a little low by the loss of large *Calanus* from the path of the smaller net, as would occur at Scoresby Sound, were the figures derived from the smaller net alone. On the other hand, however, the presence of a large crop of net-passing forms at Plymouth may result in greater fertility, all else being equal. By way of comparison with figures for the New England coastal waters given by Riley *et al.* (1949), the Scoresby Sound yearly average of 108·4 mg./m.^{3} for the

coarse-net plankton may be set against the displacement volumes (which come out a little larger than the wet weight) of 0·54 ml. (Clarke 1940) or 0·5–0·8 ml. (Bigelow & Sears 1939) for coastal water and 0·2 ml. for slope water. On the basis of the yearly average biomass, the standing crop of zooplankton at Scoresby Sound is somewhat poorer than Riley's slope water.

No phosphorus analyses were made in connexion with this work. Nielsen, however, concluded that the winter phosphate level in the East Greenland current was about 35 mg./m.^{3} or some two or three times the winter values at Plymouth in 1934. As the phytoplankton was abundant in Scoresby Sound at the end of August 1951 although not in the previous year, it seems probable that the nutrients were not exhausted by that time, or if they had been depleted that they had been renewed by the advent of the new field of ice in August. So far as we are justified in considering Nielsen's 1932–33 phosphate values in conjunction with this series of values of phytoplankton and zooplankton, we can say there is a half to a third as much plankton for a given amount of winter phosphate in Scoresby Sound as in the English Channel.

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SUMMARY

1. A study was made of the plankton throughout the year in Scoresby Sound, East Greenland, from August 1950 to 1951.

2. Fine and coarse nets fitted with meters were fished vertically through the upper 50 m. of water a mile or two offshore from the settlement at weekly or fortnightly intervals. A boat was used in summer, and in winter samples were taken through holes chipped or blown in the ice.

3. The transparency of the water was found to be at a maximum in winter and at a minimum during the melt, increasing throughout summer.

4. Phytoplankton was assessed by pigment and cell counts. Pigment values were less than 1 unit/m.^{3} throughout winter, production set in in May and high values were found in June, July and August. The yearly average net phytoplankton would be 670 units/m.^{3}, were it based on weekly samples through the year. Membrane-caught pigment in summer was less than double the net-caught pigment. Counts showed a succession of species, beginning with *Nitzschia*, *Navicula* and *Amphiprora* (associated

with thick ice), *Fragilaria* and *Thalassiosira*, passing to a population of chaetocerids, *Ceratium* and other peridinians and tintinnids in July and August. This late summer population persisted throughout the winter until the following spring. It is suggested that there is evidence of the double peak, spring and autumn, of the phytoplankton cycle of temperate waters.

5. Zooplankton organisms were assessed as wet weight according to various categories. Estimated total weights declined from 190 mg. in September to a minimum of 21 mg. at the end of March and then rose to a high average level of 391 mg./m.^{3} in July and August, the yearly average being 111·3 mg./m.^{3}. The yearly curve of abundance of the copepods is considered to be a composite effect of true population change, of migration away from the surface in late summer and towards it in spring, and of a small migration to the surface in mid-winter, in which *Calanus finmarchicus* and to a certain extent *Pseudocalanus elongatus* partake as well as *Metridia* and *Microcalanus*.

6. The respiration-rate of larger copepods at the beginning of the phytoplankton production was found to be 101·8 ml. O_2/kg. wet weight/hr.

7. It is probable that a part of the winter population is derived from production in the area of the North Pole the previous summer, but if it is assumed that the observed population changes are those which would take place in a self-contained body of water, the true rate of population decline over the winter may be tentatively estimated to be exponential at about 0·053 of the total biomass per day. It is suggested that in winter some degree of carnivorous feeding goes on as in summer, so the population can survive in the virtual absence of phytoplankton although the numbers and biomass decline.

8. The yearly average net-caught pigment, 670 units/m.^{3}, is closely similar to that in the English Channel in 1934, while on the basis of assumed phosphorus content the average standing crop of phytoplankton plus zooplankton is estimated to be of the order of two-thirds of that in the Channel.

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Table 2. *List of observations in Rosenvinge Bay, Scoresby Sound, 1950–51*

Date	Time (approx.) (hr.)	Net (F, fine; C, coarse) and no. of 0–50–0 m. hauls	Water fished ($m.^3$) and treatment (Pg, pigment; Pr, preserve) of fine net samples	Secchi disk (metres)	Method of sampling	Thickness of fast ice at hole (approx.) (cm.)	Depth of snow on fast ice at hole (approx.) (cm.)	Remarks
1950								
29 Aug.	15–17	F 1 F 1 C 1	2·72 Pg 1·70 Pr 12·10	—	From boat	—	—	Much drift ice, glass calm. Hauls with plankton sampler
21 Sept.	15–19	F 2 C 2	1·44 Pr 19·31	—	,,	—	—	Much old ice, surface covered with thin new pancake ice, calm
27 Sept.	—	—	—	17, 18, 19·5	,,	—	—	Scattered ice, much new. Clear patch of water off settlement
30 Sept.	16–19	F 2 F 2, 2 C 1	1·14 Pg 1·44, 1·21 Pr 56·4	17·5, 17·5	,,	—	—	Ice blown out yesterday, now drifting back. Samples in open water. Swarms of ctenophores seen
1 Oct.	15–19	F 2 F 2	1·44 Pg 1·24 Pr	20, 21	,,	—	—	Much new ice, loose crystals consolidating. Glass calm. Swarms of ctenophores seen
16 Oct.	12–14	F 2 C 2	1·28 Pr 24·7	—	Through hole in fast ice	15	5	Overcast, calm. Samples ½ mile offshore
18 Oct.	14–16	F 4 F 4 F 4	2·57 Pg 2·54 Pr 52·3	(19·25, 20) (Through thin ice)	,,	15	8	Haze, light wind
24 Oct.	13–15	—	—	—	,,	10	15	Clouded. W.B. worked through thin ice over frozen lead
28 Oct.	13–15	F 4 F 4 C 4	2·19 Pg 2·39 Pr 43·8	(12, through ice)	,,	15	25	Overcast, calm
16 Nov.	13–15	F 5 F 5 C 4, 4	3·02 Pg 3·18 Pr 52·3, 52·7	—		15	None	(Ice blew out 6–7 Nov. in strong N. wind) Light N.W. wind, hazy
18 Nov.	15–17	—	—	(18, through ice)	,,	30	10	Overcast
25 Nov.	15–17	F 5 F 5 C 4	2·72 Pg 3·46 Pr 62·7	(16·5, through ice)	,,	23	5	Clear with some cloud, half light

4 Dec.	13–15	—	—	(21·5, 17·5, 14·25, 12·25, 13·75 through ice)	,,	13	None	Secchi disk through hole in transparent new fast ice, 3 miles out. Half light
6 Dec.	14–16	F 5 F 5 C 4 or 5	2·82 Pg 2·98 Pr 68·5	—	,,	30	30	Overcast, slight E. wind. Half light to dark, no moon
15 Dec.	14–16	—	—	—	,,	30	23	Calm, some cloud. Air temp. about −20° C.
26 Dec.	14–16	F 5 F 5 C 5	4·21 Pg 5·25 Pr 71·2	—	,,	45	60	Sky clear, clouding. Full moon. Samples taken ¼ mile out
1951								
9 Jan.	14–16	F 5 F 5 C 5	3·88 Pg 4·24 Pr 82·9	—	,,	45	45	Calm, hoar frost depositing from mist. Half light to dark. Air temp. −20 to −30° C.
22 Jan.	15–18	—	—	—	,,	45–60	45	Hazy. Low sun at 15hr., moon at 18hr.
23 Jan.	15–19	F 5 F 5 C 5	3·36 Pg 3·88 Pr 73·1	—	,,	45–60	45	Overcast, wind slight
9 Feb.	16–17	F 4 F 5 C 5	2·54 Pg 2·87 Pr 59·9	—	,,	90	45	Samples taken 300 yd. offshore, depth 50 m. Calm, clear
26 Feb.	15–19	F 4½ F 5, 4 C 5, 5	2·64 Pg 3·02, 2·14 Pr 56·3, 61·0	—	,,	90	30	Samples taken 300 yd. offshore. Calm, becoming overcast. Air temp. −25 to −30° C.
3 Mar.	15–18	—	—	—	,,	—	—	New hole blown 1 mile offshore. Air temp. about −35° C.
8 Mar.	15–18	—	—	30 (edge of open water)	,,	—	—	Secchi disk reading at edge of ice in open water 1 mile off Cap Tobin. Air temp. −20 to −25° C.
15 Mar.	16–19	F 5 F 5, 5 C 5, 5	3·35 Pg 3·88, 3·54 Pr 84·0, 77·5	—	,,	120	45	Hole 1 mile offshore in use again. Hazy, light wind. Air temp. −15 to −20° C.
30 Mar.	17–19	F 5 F 10 C 10	3·23 Pg 5·16 Pr 155·0	—	Through hole in fast ice	120	45	Hazy, little wind. No stray on wire. Air temp. about −20° C.

Table 2 (*cont.*)

Date 1951	Time (approx.) (hr.)	Net (F, fine; C, coarse) and no. of 0–50–0 m. hauls	Water fished (m.³) and treatment (Pg, pigment; Pr, preserve) of fine net samples	Secchi disk (metres)	Method of sampling	Thickness of fast ice at hole (approx.) (cm.)	Depth of snow on fast ice at hole (approx.) (cm.)	Remarks
12 Apr.	16–19	F 5 F 10 C 10	3·76 Pg 6·80 Pr 148·0	—	,,	?120	45	Bright sun, no wind, clear. No stray on wire. Air temp. about −20° C.
18 Apr.	16–18	—	—	—	,,	?120	45	Bright sun, no wind. No stray on wire. Air temp. ? a little below freezing
29 Apr.	18–21	F 5 F 10 C 10	3·78 Pg 7·05 Pr 123·0	—	,,	120	45	Hazy, bright sun, slight wind. Air temp. about freezing. Hard crust on snow melted
12 May	16–18	F 5 F 10 C 10	3·63 Pg 7·52 Pr 143·0	—	,,	?120	30	No wind, bright sun, thaw. Sea fog later
14 May	18–21	F 4½	2·62 Pg	—	,,	—	—	Sunny, light haze, fog over sea. Light breeze. Air temp. about 0° C.
21 May	15–17	F 5 F 10 C 10	3·18 (1·22 Pg, 1·95 Pr) 6·68 Pr 139·0	—	,,	—	30	Misty, clearing later. Thaw. Snow wet
25 May	17–21	F 4½	3·38 (1·0 Pg, 1·0 Pr) (1·38 for expt.)	—	,,	—	—	Misty, light wind. Thawing
31 May	14–17	F 15½ C 10	9·95 (1·02 Pg, 8·93 Pr) 143·0	—	,,	?120	None	Overcast, breeze. Ponds of melt-water on ice. Rivulet draining into hole
5 June	17–20	F 5	3·33 (0·28 Pg, 3·05 Pr)	—	,,	—	—	Clear, half surface of sea-ice covered by 15cm. deep ponds of melt water. Rivulet draining into hole
9 June	15–19	F 14 C 10	6·46 (0·26 Pg, 6·20 Pr) 84·7	—	,,	—	—	Clear, calm to slight wind. Strong rivulet draining into hole

17 June	16–21	F 5	2·07 (0·19 Pg, 1·88 Pr)	—	,,	—	—	Clear. Ice still covered with pools of melt-water, but several holes appearing
24 June	17–21	F 15 C 10	9·82 (0·57 Pg, 9·25 Pr) 92·0	—	,,	—	—	Fast ice thin, many holes, melted near shore. Clear. (Ice blew out 29 June)
5 July	20–21	F 5	2·94 (0·17 Pg, 2·77 Pr)	9·5	From boat	—	—	Sea mist. Open water for 5 or 6 miles. Samples from 1 mile out
7 July	18–20	F 15 C 10	6·83 (0·16 Pg, 6·67 Pr) 94·3	9·75	,,	—	—	Samples 2 miles out. Clear, slight wind. Scattered pans of fiord and polar ice
8 July	17–20	F 1	1·23 (0·09 Pg, 1·14 Pr)	—	,,	—	—	Samples 2 miles out. Clear, slight wind. Much heavy ice
14 July	22–24	F 10 C 10	4·18 (0·14 Pg, 4·04 Pr) 73·1	10·0		—	—	Samples 1½ miles out. Calm, mist and rain
16 July	17–20	F 1	1·09 (0·05 Pg, 1·04 Pr)	—	,,	—	—	Samples 2 miles out. Calm. Sun obscured by high cloud
26 July	15–18	F 10 C 10	3·92 (0·26 Pg, 3·66 Pr) 74·3	11·5	,,	—	—	Samples 2 miles out. Calm to slight breeze. Sun and sea fog
29 July	16–20	F 5	1·98 (0·12 Pg, 1·86 Pr)	15·0	,,	—	—	Samples 2 miles out. Calm, some high cloud. Much ice, open pack
6 Aug.	17–19	F 5 C 5	1·84 (0·09 Pg, 1·75 Pr) 37·4	15·25	,,	—	—	Samples 2 miles out. Calm to slight N. wind. Some high cloud. Open pack
11 Aug.	18–20	F 4	1·29 (0·05 Pg, 1·24 Pr)	20·25	,,	—	—	Samples 2 miles out. Calm. Open pack. Swarms of ctenophores seen
23 Aug.	19–21	F 4 C 4	1·36 (0·09 Pg, 1·27 Pr) 24·4	9·25	,,	—	—	Samples ¾ mile out. Light wind. Sunshine slight cloud. Sound packed with heavy ice, opened up for few hours and subsequently tight again

Table 3. *Temperature and salinity*

Depth (m.)	1950					1951											
	21 Sept.	1 Oct.	24 Oct.	18 Nov.	15 Dec.	22 Jan.	3 Mar.	18 Apr.	14 May	25 May	5 June	17 June	8 July	16 July	29 July	11 Aug.	23 Aug.
								Temperature (° C.)									
1	−0·72	−1·27	−1·58	−1·74	−1·72	−1·75	−1·72	−1·69	−1·58	−1·69	−0·07	−0·02	2·08	3·36	2·28	1·74	−1·04
5	−0·87	−1·32	−1·59	−1·73	−1·76	−1·82	−1·77	−1·70	−1·69	−1·69	−1·52	−1·09	0·48	1·28	0·59	0·96	—
10	−1·04	−1·22	−1·58	−1·72	−1·77	−1·76	−1·77	−1·65	−1·68	−1·68	−1·54	−0·65	0·11	0·65	−0·13	−0·09	−1·04
15	−1·07	−1·16	−1·52	−1·73	—	—	−1·77	−1·72	−1·62	−1·62	−1·37	−0·66	−0·65	0·00	−0·38	0·16	—
20	−1·03	−1·11	−1·46	−1·72	−1·82	−1·72	−1·77	−1·72	−1·66	−1·62	−1·42	−0·97	−1·00	−0·42	−0·34	−0·22	−0·52
30	−1·02	−0·94	−1·46	−1·72	−1·76	−1·76	−1·78	−1·72	−1·68	−1·64	−1·54	−1·41	−1·59	−1·27	−0·74	−1·01	−0·39
	(43m.)				(42m.)	(42m.)	(42m.)										
40	−1·02	−0·95	−1·28	−1·72	−1·77	−1·77	−1·77	−1·72	−1·72	−1·72	−1·61	−1·62	−1·65	−1·60	−1·25	−1·46	−1·39
					(57m.)	(57m.)	(57m.)										
50	—	−0·95	−1·25	−1·72	−1·76	−1·78	−1·78	−1·72	−1·74	−1·72	−1·64	−1·67	−1·67	−1·64	−1·47	−1·55	−1·51
		(70m.)														(70m.)	
80	—	−1·02	—	—	—	—	—	−1·72	−1·80	−1·66	−1·62	−1·65	−1·62	−1·57	−1·52	−1·56	—
								Salinity (‰)									
1	22·57	29·34	30·07	32·19	—	—	32·03	31·62	31·06	31·49	5·82	10·68	26·89	29·14	28·41	24·54	28·49
5	27·33	29·62	30·47	32·21	—	—	32·03	31·64	31·69	31·54	31·48	31·33	31·20	32·07	29·96	28·58	—
10	29·83	29·80	31·06	32·23	—	—	32·44	32·44	31·97	31·70	31·54	32·25	31·69	32·34	30·55	29·31	29·29
15	30·05	30·06	31·44	32·23	—	—	32·72	32·74	32·76	32·75	32·42	32·45	32·54	32·72	30·86	30·45	—
20	30·38	30·42	31·74	32·40	—	—	32·83	32·91	32·93	32·96	32·75	32·59	32·83	32·90	31·08	31·31	29·92
30	30·07	31·55	32·23	32·39	—	—	32·99	33·02	33·11	33·06	33·04	33·12	33·31	33·24	31·82	32·66	30·81
40	—	31·85	32·46	32·48	—	—	33·06	33·17	33·18	33·19	33·22	33·39	33·46	—	32·92	33·28	33·15
50	—	32·40	32·64	32·49	—	—	32·90	33·24	33·31	33·29	33·47	33·51	33·53	33·58	33·29	33·45	33·49
		(70m.)														(70m.)	
80	—	32·60	—	—	—	—	—	33·38	33·54	33·58	33·81	33·66	33·89	—	33·81	33·71	—

Table 4. *Phytoplankton pigment and zooplankton biomass from fine and coarse net hauls*

(Combined total biomass (see text) is the sum of: the fine fraction from the fine net, the medium copepods averaged from each net, and the large copepods and other organisms from the coarse net. Figures for totals in brackets are those from which fine fraction is omitted.)

Date ...	1950										1951	
	29 Aug.	21 Sept.	30 Sept.	1 Oct.	16 Oct.	18 Oct.	28 Oct.	16 Nov.	25 Nov.	6 Dec.	26 Dec.	9 Jan.	23 Jan.
FINE NET HAULS													
Phytoplankton pigment (units/m.³)													
Net	<10	<10	10·4	10·0	—	1·0	5·8	4·9	<0·28	<0·21	0·25±0·1	0·45±0·2	0·87
Membrane—from same station	—	—	—	—	—	—	—	—	—	—	—	—	—
Zooplankton biomass (mg./m.³)													
Fine fraction	22·9	90·0	44·7	72·7	60·8	18·5	33·0	25·4	16·4	13·4	7·4	14·2	23·1
Medium fraction copepods	20·6	46·0	17·8	19·4	9·4	10·6	8·0	10·4	3·8	5·7	3·2	5·7	5·7
Coarse fraction copepods	51·7	44·0	24·2	22·6	7·8	3·9	9·0	6·0	2·3	2·0	8·6	2·5	2·8
Organisms other than copepods	17·2	17·0	54·6	18·2	2·3	3·9	15·0	2·2	—	2·0	—	0·5	1·6
Total zooplankton biomass	112·4	197·0	141·3	132·9	80·3	36·9	65·0	44·0	22·5	23·1	19·2	22·9	33·2
COARSE NET HAULS													
Zooplankton biomass													
Medium fraction copepods	25·0	25·1	10·4	—	9·3	14·7	12·9	8·7	3·5	4·0	2·8	1·9	2·1
Coarse fraction copepods	116·0	47·8	41·4	—	10·5	8·9	16·7	8·8	3·1	7·0	8·5	9·4	5·6
Sagitta	3·1	3·9	5·2	—	0·8	—	1·5	0·3	0·6	1·2	1·5	0·4	1·1
Amphipoda	9·8	0·5	0·02	—	0·04	—	0·05	—	—	—	0·1	0·2	0·4
Other Crustacea	—	—	0·02	—	—	—	—	—	0·03	0·1	—	—	—
Young fish	—	—	—	—	—	—	—	—	—	—	—	—	—
Fish eggs	—	—	—	—	—	—	—	—	—	—	—	—	—
Limacina	—	—	—	—	—	—	—	—	—	—	—	0·05	—
Clione	—	—	—	—	—	—	—	—	—	—	—	—	—
Oikopleura	7·5	3·4	17·7	—	0·04	—	8·2	0·4	0·4	0·06	0·1	—	0·01
Fritillaria	—	—	—	—	—	—	—	—	—	—	—	—	—
Medusae, Ctenophora, Scyphozoa, Siphonophora	0·4	5·8	0·3	—	18·2	—	8·3	1·6	11·7	0·4	8·0	0·7	—
Collozoum	—	—	—	—	—	—	—	—	—	0·1	—	—	—
Unidentifiable gelatinous matter	—	2·5	—	—	—	—	—	—	—	—	—	—	—
Total zooplankton biomass	161·8	89·0	75·0	—	38·9	23·6	47·6	19·8	19·3	12·9	21·0	12·6	9·2
TOTAL BIOMASS, combined from fine and coarse nets	182·5	189·5	123·4	—	99·8	40·1	79·2	46·1	35·9	27·2	28·6	28·7	34·1

Table 4 (*cont.*)

Date ...	1951 9 Feb.	26 Feb.	15 Mar.	30 Mar.	12 Apr.	29 Apr.	12 May	14 May	21 May	25 May	31 May	5 June	9 June
FINE NET HAULS													
Phytoplankton pigment (units/m.³)													
Net	1·0±0·3	<0·23	<0·1	0·2±0·1	0·38±0·2	<0·16	10·8	17·6	541	129	117	1950	3240
Membrane—from same station	—	—	—	—	—	—	—	—	—	—	—	2200	—
Zooplankton biomass (mg./m.³)													
Fine fraction	8·9	19·1	11·5	9·9	12·4	19·4	23·4†	—	—	—	—	—	—
Medium fraction copepods	4·2	3·1	2·3	1·7	2·8	3·7	2·7	—	3·7	—	7·5	—	12·6
Coarse fraction copepods	7·0	6·7	0·1	0·8	0·3	1·6	4·0	—	4·3	—	8·0	—	8·7
Organisms other than copepods	1·0	—	—	—	—	—	3·0	—	1·4	—	0·4	—	2·8
Total zooplankton biomass	21·1	28·9	13·9	12·4	15·5	24·7	33·1	—	(9·4)	—	(15·9)	—	(24·1)
COARSE NET HAULS													
Zooplankton biomass													
Medium fraction copepods	2·0	2·8	3·3	1·7	1·9	5·3	3·5	—	6·3	—	9·0	—	17·0
Coarse fraction copepods	9·6	4·6	3·1	1·3	2·4	3·2	7·9	—	13·1	—	21·6	—	45·2
Sagitta	0·4	1·0	0·6	0·1	0·9	0·2	0·1	—	0·2	—	0·3	—	0·3
Amphipoda	1·3	—	—	8·0	5·6	—	—	—	0·8	—	0·2	—	0·5
Other Crustacea	—	—	—	—	—	—	—	—	—	—	—	—	—
Young fish	—	—	—	—	—	0·02	—	—	1·08	—	0·55	—	0·9
Fish eggs	—	—	—	—	—	—	—	—	—	—	—	—	—
Limacina	—	—	—	—	—	—	—	—	0·1	—	—	—	1·6
Clione	—	—	—	—	—	—	—	—	0·02	—	—	—	1·5
Oikopleura	—	—	0·03	—	0·2	0·03	0·04	—	0·3	—	0·4	—	3·1
Fritillaria	—	—	—	—	—	—	—	—	—	—	—	—	—
Medusae, Ctenophora, Scyphozoa, Siphonophora	5·2	0·9	11·4	0·1	200·8	9·5	0·6	—	0·7	—	4·1	—	49·6
Collozoum	0·3	—	—	0·1	—	—	—	—	—	—	—	—	—
Unidentifiable gelatinous matter	—	—	4·6	—	—	—	—	—	—	—	0·19	—	6·3
Total zooplankton biomass	18·8	9·3	23·1	11·3	211·8	18·3	12·1	—	22·6	—	36·4	—	126·0
TOTAL BIOMASS, combined from fine and coarse nets	28·8	28·6	34·1	21·2	224·7	36·9	35·1	—	(21·3)	—	(35·7)	—	(123·8)

† Weighings of fine fraction discontinued.

Date ...	1951 17 June	24 June	5 July	7 July	8 July	14 July	16 July	26 July	29 July	6 Aug.	11 Aug.	23 Aug.	Average for the year
						FINE NET HAULS							
Phytoplankton pigment (units/m.³)													
Net	1860	1820	2780	2780	3350	5200	8850	692	1670	660	3580	2570	670*
Membrane—from same station	3770	—	—	—	3600	—	9250	—	4800	—	4000	4360	—
Zooplankton biomass (mg./m.³)													
Fine fraction	—	—	—	—	—	—	—	—	—	—	—	—	—
Medium fraction copepods	—	45·0	—	44·3	—	31·9	—	63·0	—	85·2	—	69·0	18·9
Coarse fraction copepods	—	15·6	—	48·5	—	70·7	—	—	—	71·0	—	28·0	15·9
Organisms other than copepods	—	—	—	203·0	—	35·4	—	31·7	—	22·9	—	0·5	15·1
Total zooplankton biomass	—	(60·6)	—	(295·8)	—	(138·0)	—	(94·7)	—	(179·1)	—	(97·5)	(49·9)
						COARSE NET HAULS							
Zooplankton biomass													
Medium fraction copepods	—	36·9	—	31·8	—	34·9	—	21·8	—	47·8	—	101·0	16·0
Coarse fraction copepods	—	15·7	—	125·7	—	192·1	—	11·8	—	139·0	—	111·0	35·4
Sagitta	—	0·2	—	1·7	—	6·0	—	1·2	—	7·5	—	0·7	1·47
Amphipoda	—	0·01	—	4·0	—	1·3	—	0·9	—	8·2	—	2·9	1·60
Other Crustacea	—	0·09	—	—	—	—	—	—	—	—	—	—	0·008
Young fish	—	—	—	0·03	—	—	—	—	—	—	—	—	0·09
Fish eggs	—	—	—	—	—	—	—	—	—	—	—	—	0·002
Limacina	—	—	—	—	—	0·26	—	0·65	—	12·0	—	—	0·55
Clione	—	—	—	—	—	—	—	—	—	—	—	—	0·05
Oikopleura	—	0·7	—	9·0	—	30·8	—	23·9	—	37·6	—	42·6	6·64
Fritillaria	—	—	—	—	—	—	—	184·0	—	17·6	—	43·0	8·74
Medusae, Ctenophora, Scyphozoa, Siphonophora	—	0·1	—	4·5	—	2·6	—	3·0	—	20·6	—	29·9	14·3
Collozoum	—	—	—	—	—	—	—	—	—	—	—	—	0·018
Unidentifiable gelatinous matter	—	3·2	—	47·9	—	48·6	—	341·6	—	132·2	—	71·8	23·5
Total zooplankton biomass	—	56·9	—	224·7	—	316·6	—	588·9	—	422·6	—	402·9	108·4
TOTAL BIOMASS, combined from fine and coarse nets	—	(61·0)	—	(231·1)	—	(315·1)	—	(339·5)	—	(341·3)	—	(387·4)	—

* Figure for average plant pigment obtained by interpolating weekly catches of zero pigment in winter.

Table 5. *Net phytoplankton*

(Cells/m.^{3}; figures in heavy type, cells/litre. + = present but not determined quantitatively; usually scarce, seen in further fractions of sample.)

	1950									1951				
Date	29 Aug.	21 Sept.	30 Sept.	16 Oct.	28 Oct.	16 Nov.	25 Nov.	6 Dec.	26 Dec.	9 Jan.	23 Jan.	9 Feb.	26 Feb.	15 Mar.
Volume examined (l.) ...	100	10	100	200	100	100	500	500	200	200	200	500	500	500
DIATOMS														
Melosira hyperborea (Grun.)	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hyalodiscus stelliger Bailey	—	—	—	—	—	—	2	—	—	—	—	2	—	—
Coscinodiscus ? subtilis Ehr.	10	+	40	30	10	10	—	—	—	+	—	—	—	2
Thalassiosira Nordenskioldii Cleve	—	—	—	—	—	—	—	—	—	—	—	—	—	—
T. gravida Cleve	—	+	—	—	—	—	—	—	—	—	—	—	—	—
Lauderia glacialis (Grun.)	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bacteriosira fragilis Gran	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Dactyliosolen antarcticus Castr.	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Rhizosolenia styliformis Brightw.	—	200	230	—	20	120	—	—	—	—	—	2	2	—
R. hebetata (Bail.), f. *semispina* Hansen	—	—	30	—	—	—	—	—	—	—	—	—	—	—
f. *hiemalis* Gran	—	—	30	—	—	—	—	—	—	—	—	—	—	—
Chaetoceros atlanticus Cleve	—	—	240	10	—	—	—	—	120	190	40	—	14	14
C. densus Cleve	100	900	610	200	10	300	44	42	—	+	—	76	26	22
C. borealis Bailey	50	—	70	—	10	200	—	—	—	+	15	—	2	—
C. convolutus Castr.	—	—	40	+	80	90	14	—	—	35	—	16	20	4
C. concavicornis Mangin	40	—	1580	140	—	50	12	26	30	30	10	—	—	—
C. decipiens Cleve	6580	3300	810	1690	34030	1920	720	274	340	1250	730	520	572	300
C. subtilis Cleve	—	4800	—	—	—	—	—	—	—	—	—	—	—	—
C. debilis Cleve	36	61400	74900	2130	2640	930	106	60	—	95	—	22	—	6
C. gracilis Schütt	—	—	—	+	—	—	—	—	—	5	—	—	—	4
Biddulphia arctica (Brightw.)	—	—	—	—	—	—	—	—	—	—	—	2	—	—
Eucampia greenlandica Cleve	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Fragilaria oceanica Cleve	—	—	—	—	—	160	—	60	—	—	—	—	—	—
F. cylindrus Grun.	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Achnanthes taeniata Grun.	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Navicula septentrionalis (Grun.)	—	—	—	—	—	—	—	—	—	—	—	—	—	—
N. Granii (Jörgensen)	—	—	—	—	—	—	—	—	—	—	—	—	—	—
N. pelagica Cleve	—	—	—	—	—	—	—	—	—	—	—	—	—	—
N. Vanhoffeni Gran	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bottom naviculids	—	+	—	—	—	—	—	—	—	—	—	—	—	—
Gyrosigma sp.	—	—	10	—	—	—	—	—	—	—	—	—	—	—
Amphiprora hyperborea (Grun.)	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Nitzschia frigida Grun.	—	—	—	—	—	—	—	—	—	—	—	—	—	—
DINOFLAGELLATES	(from 500 l.)	(from 50 l.)												
Ceratium arcticum Ehr.	138	860	10	210	460	230	10	12	310	385	45	52	62	46
Dinophysis sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Other thecate peridinians	84	140	170	—	40	10	—	4	40	30	40	8	5	6

Other flagellates														
Dinobryon	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Phaeocystis	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Halosphaera	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Carteria sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ciliates														
Cyttarocylis spp. (*gigantea* Brandt, *media* Brandt, *cuspidata* Meunier)	40	400	650	440	10	130	8 (from 200 l.)	6 (from 200 l.)	40	110	35	22	10	8
Ptychocylis obtusa Brandt	10	100	500	180	430	960	310	700	1120	1960	2375	524	710	186
Tintinnus secatus Brandt	—	—	10	—	—	—	—	—	+	10	20	6	—	4
T. pellucidus Meunier	—	—	—	—	—	—	—	—	—	—	—	—	—	—
T. gracilis Brandt	—	—	+	—	—	—	—	—	—	—	—	—	—	—
T. vitreus Brandt	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Tintinnopsis sp. (close to *nitita* Brandt)	—	—	—	—	—	—	—	—	—	40	30	—	—	—
Radiolaria	155	—	+	—	—	—	—	—	—	—	—	—	—	—
Foraminifera	—	—	—	—	—	10	—	—	—	—	—	—	—	—

1951

Date	30 Mar.	12 Apr.	29 Apr.	12 May	21 May	31 May	9 June	24 June	7 July	14 July	26 July	6 Aug.	23 Aug.
Volume examined ...	500 l.	200 l.	200 l.	50 l.	1 l.	5 l.	100 c.c.	50 c.c.	100 c.c.	100 c.c.	250 c.c.	250 c.c.	100 c.c.
Diatoms													
Melosira hyperborea	—	—	—	—	+	**9**	**120**	—	**20**	—	+	—	—
Hyalodiscus stelliger	—	—	—	—	—	—	—	—	—	—	—	—	—
Coscinodiscus ? subtilis	2	15	—	+	+	+	—	—	—	—	+	—	+
Thalassiosira Nordenskioldii	—	—	130	—	**80**	**21**	**1760**	**6140**	**1190**	**3240**	**172**	**24**	—
T. gravida	—	10	180	200	**197**	**31**	**1650**	**6120**	**2820**	**4510**	**100**	**312**	—
Lauderia glacialis	—	—	—	—	—	+	**20**	—	—	+	—	—	—
Bacteriosira fragilis	—	—	—	—	—	+	**20**	**40**	**190**	+	+	—	—
Dactyliosolen antarcticus	—	—	—	—	—	—	—	—	—	—	—	—	—
Rhizosolenia styliformis	—	—	—	—	—	—	—	—	—	—	—	—	—
R. hebetata f. *semispina*	—	—	—	—	—	—	—	—	—	—	—	—	+
f. *hiemalis*	—	—	—	—	—	—	—	—	—	—	—	—	—
Chaetoceros atlanticus	54	15	40	—	—	—	—	+	—	+	—	**8**	—
C. densus	—	—	—	—	—	—	—	—	—	—	—	—	—
C. borealis	—	—	10	—	+	—	—	**220**	—	**20**	**12**	**12**	+
C. convolutus	24	—	—	—	—	—	—	—	+	—	**28**	—	**240**
C. concavicornis	—	—	—	—	—	—	—	—	—	+	—	—	**40**
C. decipiens	98	180	390	360	**15**	**2**	**30**	**320**	**290**	**110**	**396**	**548**	**1280**
C. subtilis	—	—	—	—	—	—	—	—	—	—	—	—	—
C. debilis	—	—	120	—	+	**2**	**840**	**83420**	**320**	**150**	**556**	**1260**	**2920**
C. gracilis	—	—	—	—	—	—	—	—	—	—	—	—	—
Biddulphia arctica	—	+	—	—	+	—	+	—	—	—	—	—	—
Eucampia greenlandica	—	—	—	—	—	+	—	—	**30**	**200**	**56**	—	—
Fragilaria oceanica	126	—	14360	—	**9591**	**8082**	**78810**	**35600**	**7350**	**10050**	**660**	**188**	—

Table 5 (*cont.*)

	1951												
Date	30 Mar.	12 Apr.	29 Apr.	12 May	21 May	31 May	9 June	24 June	7 July	14 July	26 July	6 Aug.	23 Aug.
Volume examined ...	500l.	200l.	200l.	50l.	1l.	5l.	100c.c.	50c.c.	100c.c.	100c.c.	250c.c.	250c.c.	100c.c.
Fragilaria cylindrus	—	—	—	—	—	—	—	—	—	—	**120**	—	—
Achnanthes taeniata	—	—	—	—	—	—	—	—	+	—	—	—	—
Navicula septentrionalis	—	—	150	4300	**30**	—	—	—	—	—	—	—	—
N. Grani	—	—	120	260	—	—	—	—	—	—	—	—	—
N. pelagica	—	—	—	1000	**30**	**7**	**150**	—	—	**500**	—	—	—
N. Vanhoffeni	—	—	—	—	**20**	**8**	—	—	—	—	**2128**	—	—
Bottom naviculids	—	—	—	—	+	**2**	—	—	+	—	+	—	+
Gyrosigma sp.	—	—	—	—	—	—	+	—	—	—	+	+	—
Amphiprora hyperborea	—	—	260	1540	**112**	**65**	**400**	—	—	**160**	**12**	+	—
Nitzschia frigida	—	—	1900	15700	+	**27**	—	**40**	—	+	+	+	+
DINOFLAGELLATES					(from 50 l.)	(from 50 l.)		(from 100 l.)		(from 50 l.)		(from 50 l.)	(from 50 l.)
Ceratium arcticum	70	190	280	580	+	600	+	190	—	600	+	740	+
Dinophysis sp.	—	—	—	—	—	—	—	—	—	—	—	20	—
Other thecate peridinians	4	30	100	40	480	1080	+	1040	+	2160	(from 50 l.) 11600	20380	12660
OTHER FLAGELLATES													
Dinobryon	—	—	—	—	2000	—	—	—	—	—	—	+	—
Phaeocystis	—	—	—	—	—	+	+	+	—	—	—	—	—
Halosphaera	—	—	—	—	—	—	—	—	+	—	+	+	—
Carteria sp.	—	—	—	—	—	—	—	—	—	+	+	—	+
CILIATES													
Cyttarocylis spp. (*gigantea* Brandt, *media* Brandt, *cuspidata* Meunier)	20 (from 200 l.)	15	15	—	10	20	—	10	+	260	1400	940	1840
Ptychocylis obtusa Brandt	190	210	100	—	60	240	10	610	+	1260	52000	6960	2060
Tintinnus secatus Brandt	25	—	15	20	—	—	—	—	+	20	—	—	—
T. pellucidus Meunier	—	—	—	—	—	—	—	—	—	20	—	20	—
T. gracilis Brandt	—	—	—	+	—	—	—	—	—	—	—	—	20
T. vitreus Brandt	2	—	—	+	—	20	—	—	—	—	+	+	+
Tintinnopsis sp. (close to *nitita* Brandt)	—	—	—	—	—	100	—	10	+	40	+	60	20
RADIOLARIA	—	—	—	—	—	20	—	10	—	1740	+	1360	220
FORAMINIFERA	—	—	—	—	—	—	—	—	—	—	—	—	—

A NEST-RECORDING DEVICE

By R. J. FANT

I.C.I. Game Research Station, Fordingbridge

(With Plate 5 and 3 Figures in the Text)

The apparatus to be described was designed primarily for the purpose of recording the movements of a wild partridge on her nest during the periods of laying and incubating her clutch. The work was undertaken as part of the activities of the I.C.I. Game Research Station with the object of adding to the existing knowledge of the habits of wild game birds. Direct observation of a wild partridge's nest presents great difficulties since the presence of a hide close enough to be effective might result in abnormal behaviour or desertion on the part of the bird, and such observation could only be carried out during the hours of daylight. It was therefore necessary to produce an automatic device which would time the movements of the bird on and off its nest. It is essentially an electrical device powered by a car battery and consists of a simple make and break switch connected to a recording unit by a twin wire cable. The particular apparatus was designed to provide for up to six simultaneous recordings. With modifications the device could be used for recording the nesting activities of smaller or larger birds.

The nest switch (Fig. 1) is a modified jack switch having two steel contacts, the upper arm of which is extended to form a lever, which when placed in position projects into the edge of the nest. Depression of this lever by the sitting bird causes the switch points to make contact and produce a closed circuit. The switch contacts are of flat spring steel $\frac{1}{4}$ in. wide and the contact points gap should be such as to connect only on a positive movement of about half an inch at the tip of the lever. The setting of this gap will determine the degree of restlessness recorded by the bird, but it is important to realize that the closer the gap is set the more chance there is of some object of vegetation near the switch causing the spring return to become inoperative. The extended lever which makes actual contact with the body of the bird must be well insulated to prevent the danger of irritating shocks to the bird during wet weather, and this can be effected by binding it with raffia; alternatively, the lever can be placed in the negative side of the circuit. The cover which shrouds the switch unit is of Perspex sheet, and was added after tests in the field had shown that the condensation of moisture on an open switch tended to form at the end distal to the nest, flow towards the contact points and there produce a short circuit. The terminal end of the cover is sealed with wax. In practice it will be found of advantage to camouflage this part of the recorder, and this is best done by brushing a quick-drying waterproof adhesive over the external parts, and when tacky adding pieces of leaves and grasses till the switch blends with the surroundings of the nest. The switch was secured in position by clamping the body to a square wooden stake which was driven into the ground near the nest. The clamp should be such as to allow for adjusting the angle of the switch after the stake has been fixed.

The presence of this stake and the body of the switch seemed to have little effect on the behaviour of the birds recorded. In fact nest switches without any camouflage have been successfully used (Pl. 5*A*), but the position of the tip of the lever must be carefully considered to avoid unduly impeding the movements of the bird while sitting. It is believed that the hen partridge turns her eggs by a series of rotational movements of her body, and for this reason the lever was placed so as to project only an inch inside the edge of the nest.

From the nest switch a twin cable leads to the recording unit which for most purposes should be placed a reasonable distance from the nearest nest to avoid the necessity of approaching the nest area when collecting records. The strategic placing of the recorder is of great importance where more than one nest is being recorded

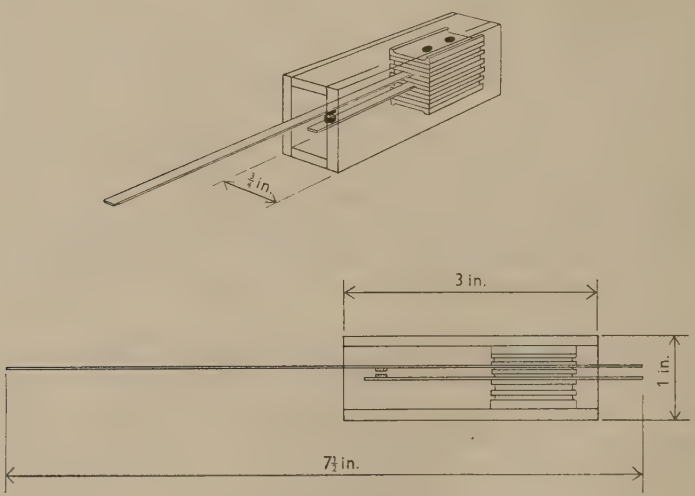
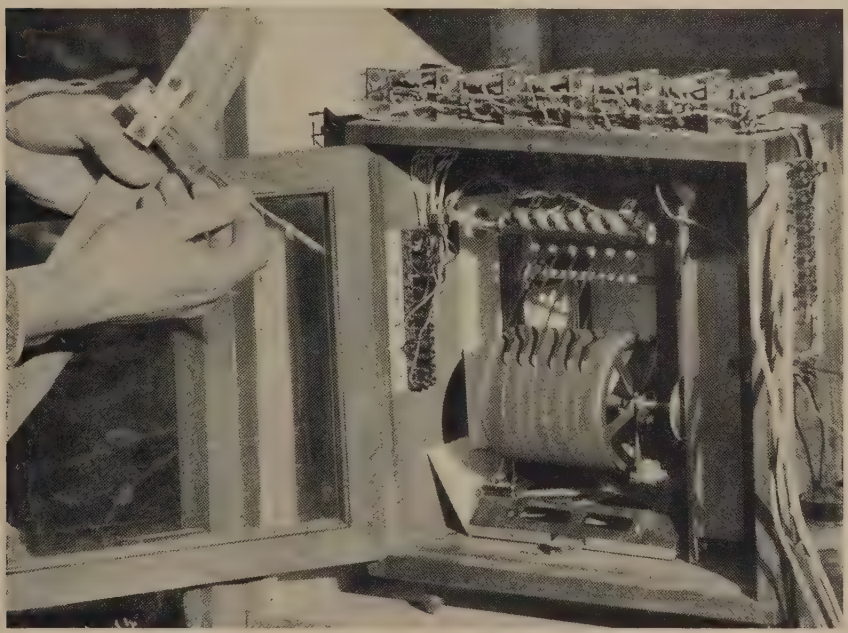


Fig. 1. The nest switch.

both as regards the cable lengths involved and the desirability of concealing the recorder box from curious humans. The length of cable which it is practical to use will depend on its resistance, the voltage available, and the current in the circuit. When the apparatus is operated from a 6 V., 100 amp.-hr. car battery, 100 ft. of 'DON 8' twin telephone cable can be used in each circuit, and records can be taken from six nests at the same time.

The recording unit (Pl. 5*B*) consists of a clockwork-operated kymograph drum, bearing smoked glazed paper and geared to make one complete revolution in 24 hr. Hinged above the drum is a unit of six magnetic markers with their pointers adjusted to make a light contact with the surface of the recording drum. The coils of each of these markers have a resistance of 16 Ω and will operate at 4 V. These coils constitute the greatest drain on the current resources of the apparatus. It was found difficult to increase the resistance of these coils (and thus reduce the consumption) at the voltage available without unduly increasing the cost and so a series of relays were incorporated to effect an economy in current consumption. The six relays mounted

A, a naked nest switch in a partridge's nest taken immediately after the bird had led her brood off.



B, the recording unit. Cables from the nest switches enter the terminals on the right; the terminal block numbered 1–6 on the left connects the relays with the markers.

on top of the case have each a coil resistance of 46 Ω. Each relay incorporates two switches, one normally made contact and one normally open contact (Fig. 2). It is thus possible to control the action of the nest switch on the magnetic markers so that a minimum of current is used for the particular phase being recorded. Thus during the recording of egg-laying the open relay switch was in circuit so that current flowed in the marker coils only when the bird was on the nest in the act of laying an egg. This period amounted to less than 1 hr. per day. On the other hand, during the incubating phase the closed relay switch was used so that current flowed in the marker coil only during the relatively short periods when the bird was off the nest for feeding and recreation. By means of the two-pole terminal block placed in circuit between the relay switches and the marker coils the change over from one switch to the other can be effected in a few seconds. Provision was made for smoking and varnishing papers on the spot, as the transport of smoked papers present difficulties. The whole of the recording unit together with the battery and other gear was housed in a weatherproof box with a door secured by a padlock.

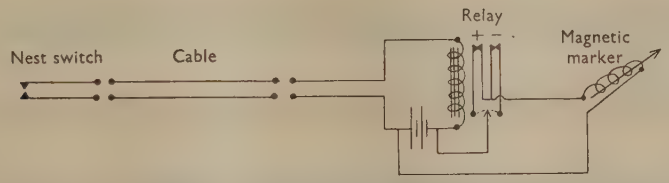


Fig. 2. Circuit diagram of the recorder.

RESULTS

Records made of four wild partridges' nests, whilst insufficient to provide a complete picture, have nevertheless given some interesting figures. The birds recorded were *Perdrix p. perdrix* nesting in sites on an experimental estate near Fordingbridge.

(*a*) *The period of egg-laying*

The hen visited her nest only for egg-laying and did this between the hours of 9.30 a.m. and 3.0 p.m. In the process of egg-laying she remained on her nest for an average period of 45 min. and did not vary this time more than ± 10 %. Whilst the bird was on the nest the switch was frequently depressed and released, indicating that she did not remain quiescent during the period (Fig. 3).

(*b*) *The incubation period*

The four partridge hens recorded showed a striking similarity in their recordings. Absences from the nest for recreation and feeding varied from two to five periods per day, the earliest being at 7.30 a.m. and the latest at 9.15 p.m. Most of the periods of absence fell between the hours of 10 a.m. and 7.0 p.m. and the duration of these absences ranged from 15 to 55 min. It was found that the greater the number of times the hen left her nest per day the shorter were the periods; the total average duration of the absences per day was 140 min. When these results were correlated with the weather it was found that during cold and inclement weather their daily periods of

recreation were of shorter duration, and more frequent; on the other hand, warm spells produced less frequent but longer periods of absence. During a period of continuous rain on 4 and 5 June 1952 not only did the birds fail to leave their nests throughout the wet spell of 36 hr., but even ceased to record their normal restless movements.

(*c*) *The transition period from laying to incubation*

The recordings afforded a possible explanation of the belief held by gamekeepers that wild partridges often take a period of 28–30 days to incubate a clutch instead of the accepted 23 to 24 days. Incubation periods are usually calculated from the time

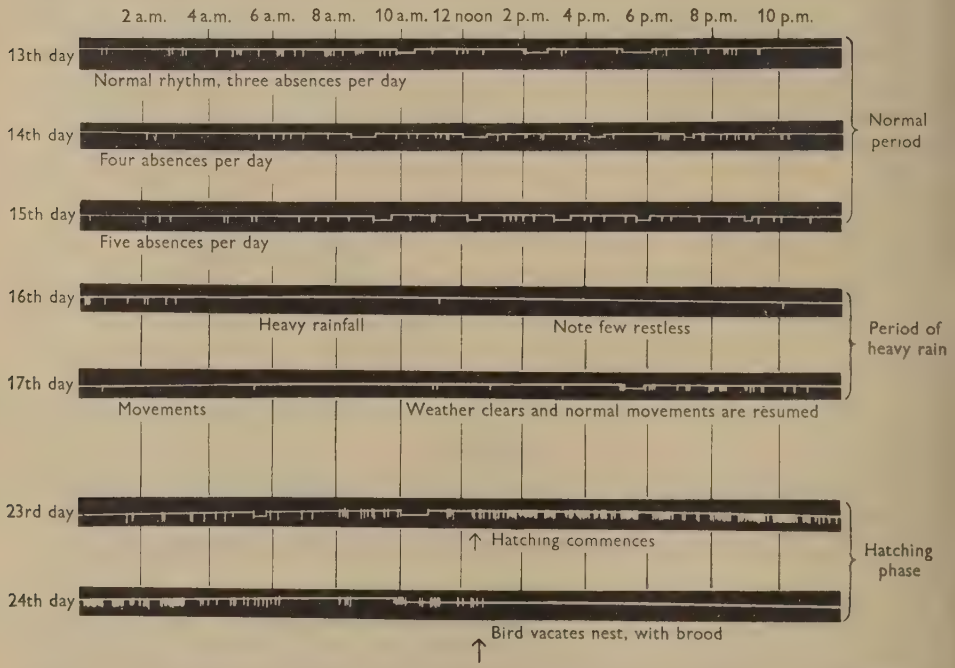


Fig. 3. Recordings of a hen partridge during three phases of the incubation period. Upper horizontal line indicates bird sitting, lower horizontal line bird absent. Vertical lines show restlessness.

the hen 'opens her nest', i.e. arranges her eggs in the normal position for sitting, to the time she leads her brood of chicks off. The recordings showed that the completion of this act of opening the nest did not always coincide with the commencement of incubation. One bird opened her nest but did not commence sitting for three days afterwards, although she visited the nest for one short period each day in between.

(*d*) *The final phase of the incubating period*

About 20 hr. before the birds led their broods off they left their nests for the final recreational period. The onset of the hatching period is shown in the recordings by a great increase in the restless movements. During the whole of this period the switch was in almost continuous motion up and down, and visual observation of the nest

during this period showed that the chicks themselves were responsible for a good deal of this recorded movement. The birds recorded left their nests for recreation and feeding for the last time between 9 a.m. and 3 p.m., hatched their broods throughout the night, and led them off between 10 a.m. and 2 p.m. the next day.

SUMMARY

In the course of investigating the behaviour of wild partridges in the field, an apparatus was devised to record the movements of the hen on and off her nest during the laying and incubating periods. Records obtained from four nesting birds show the periodicity of egg laying, the number and the duration of absences from the nest during the incubating phase, and the bird's reactions to variations in local climatic conditions.

THE EFFECT OF LOWERED SALINITY ON SOME BARNACLE NAUPLII

By H. BARNES

The Marine Station, Millport

(With 1 Figure in the Text)

That adult *Balanus balanoides* (L.) and *B. crenatus* Brug. can withstand large salinity fluctuations over considerable periods of time has been established by Kreps and his colleagues (Kreps 1929; Borusk & Kreps 1929). They demonstrated that at a salinity of about 6‰ motor activity of the cirri ceased, respiration fell to a low level, possibly with the accumulation of an oxygen debt, and the animal remained in what was termed a state of 'salt sleep'. In this state the animals survived fresh water for three weeks. Cirral beating was virtually normal at 12‰ salinity. Poulsen (1935) has also reported the occurrence of the former species in 14‰ salinity and the latter at 9‰. Such a capacity to withstand changes in salinity over moderately long periods of time is clearly of important survival value in littoral species such as *B. balanoides* and *B. crenatus*, which extends to the littoral fringe. However, these two species, and *B. balanus* (L.) da Costa are not usually considered euryhaline species as is, for example, *B. improvisus* Darw. (Broch 1924), and this position was maintained by Schaper (1922) who pointed out that *B. balanoides* does not penetrate the Baltic Sea. It is clear from the work of Stephensen (1933) that around Denmark *B. balanus* does not penetrate as far into the Baltic as does *B. crenatus*.

It might be expected that in animals with planktonic larvae the ability of the larvae, in the first instance the early stages, to withstand changes of salinity would be of considerable importance in determining the distribution of the species with respect to salinity, and a comparison has therefore been made between the early stage nauplii of *B. balanoides*, *B. crenatus* and *B. balanus* in their reactions to changes of salinity.

In all cases stage I nauplii were obtained by opening ripe adults and teasing the contents out into finger bowls under sea water. Large numbers of active nauplii were thereby liberated. Samples of nauplii were collected after aggregating the nauplii at the side of the dish with a spotlight, and these were transferred to a series of small dishes containing solutions of graded salinity prepared by adding distilled water to outside sea water. After remaining in these solutions for varying known periods, during which observations were made on the activity of the nauplii, they were transferred back to normal sea water (unless fully active) and examined at intervals for recovery. After the necessary intervals the samples were fixed and then counted. In a further series of experiments the nauplii were first transferred to normal sea water and distilled water added over a period so that the salinity was only gradually changed. In all cases adequate controls were run, and only those observations are recorded for which the controls gave 95–100% survival over the whole experimental period. The experiments were all carried out at uncontrolled room temperature (about 15° C.), and the test animals were kept out of direct sunlight.

The results are shown in diagrammatic form in Fig. 1. In *B. balanoides* a sudden change of salinity over the range 30‰ down to 18‰ had no effect; the nauplii remained vigorous throughout, moulting normally to the stage II even when remaining in the solution up to 62 hr. Beyond the lower salinity of this range the survival was markedly dependent upon the time of immersion in the solution. The nauplii were killed by 2 min. immersion in fresh water and in 1 hr. in 3‰ salinity. Immersion for 10 min. at a salinity of 6‰ gave, except for a slight occasional twitching of the limbs, complete cessation of movement, but on return to normal sea water recovery was

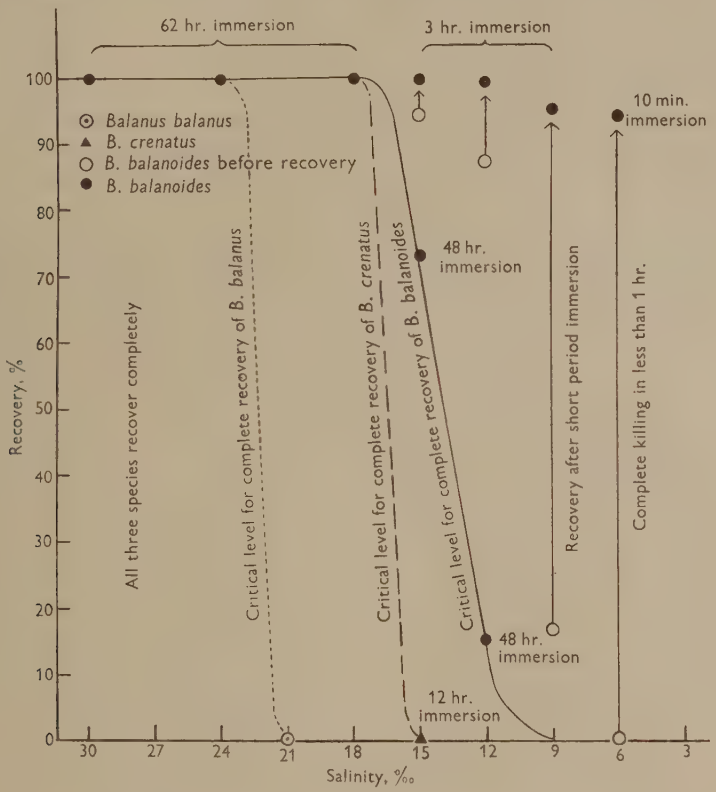


Fig. 1. The effect of various salinities on *Balanus* nauplii.

complete. Increasing the time of exposure to this salinity gave a gradual increase in the numbers killed, until after 14 hr. in this solution no recovery took place. At 9‰ salinity cessation of movement again occurred, but recovery was complete even after 3 hr. In 12‰ salinity the effect was the same, virtually complete cessation of movement, but even after 24 hr. recovery was complete. However, after 48 hr. in this solution only 12% of the nauplii recovered, but only partially for the activity was much reduced. At 15‰ there was 73% recovery, even after 48 hr. immersion.

The behaviour of the other two species was similar; there was a lower salinity limit beyond which recovery was dependent upon the total time of immersion in the solution

and above which there was no observable effect. In the case of the nauplii of *B. crenatus* the limit for complete recovery appears to be rather higher than for *B. balanoides*, namely at 15‰, and even higher still, 21–24‰ for *B. balanus*.

The effect of reducing the salinity gradually was in all cases to reduce its effect in killing the nauplii. Thus at a salinity of 3‰ *B. balanoides* nauplii after 1 hr. immersion directly into the solution gave only 8% recovery and this very incompletely, whilst when the salinity was gradually reduced to this value over a period of an hour, 93% recovered on returning to normal sea water, after remaining at 3‰ salinity for 1 hr. Again, with *B. crenatus* nauplii after a gradual reduction to 3‰ and maintaining at this salinity for 10 min. gave 96% recovery, whilst rapid transfer to this salinity for 10 min. gave only 12% recovery.

It should be pointed out that in the resting state, as when in a solution of low salinity, development is delayed since, although on returning to normal sea water full activity is regained, little development to stage II takes place under the conditions of quiescence.

DISCUSSION

The results indicate quite clearly that the salinity range tolerated by the nauplii of the three species could be of considerable importance in determining their distribution. None of the species is likely to spread into water of salinity much lower than 16‰ unless a distinct brackish water race were developed in it. Short periods of exposure to water of lower salinity could be tolerated by *B. balanoides* and *B. crenatus*. Although the results for *B. balanus* may be due to some extent to the lowered viability of the larvae, due to keeping dredged material under artificial conditions, it would seem that its nauplii are less resistant to lowered salinity than those of the other two species. Between *B. balanoides* and *B. crenatus* there is less difference, the former in these experiments showing somewhat greater resistance to any deleterious effects of lowered salinity.

In general, the known distribution of the three species, particularly where it can be followed through a salinity gradient, as in the case of the Skagerrak, Kattegat and Baltic, is in agreement with the suggestion that it is determined by the tolerance of the nauplii to lower salinities. Thus, *B. crenatus* extends to the waters off the south-east coast of Sweden, whilst *B. balanus* is not found east of the Kattegat according to Stephensen (1933). *B. balanoides* extends into the coasts of the Kattegat but does not penetrate into the Baltic Sea.

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CHANGES IN THE ORIENTATION OF BARNACLES OF CERTAIN SPECIES IN RELATION TO WATER CURRENTS

By D. J. CRISP
Marine Biological Station, University College of North Wales, Bangor

(With Plate 6 and 6 Figures in the Text)

INTRODUCTION

In 1933 Moore drew attention to the curvature of the radial canals in the basis of *Balanus improvisus* Darwin, and pointed out that this curvature could only have resulted from a rotation of the axis of the shell in the course of growth. Although direct observation of a change in orientation of the axis was not made, it is difficult to refute the logic of this argument. On the other hand, Barnes, Crisp & Powell (1951) have shown that there is no observable change of orientation during growth in *B. crenatus*, *B. balanoides* and *Elminius modestus*. None of these species has a porous basis like that of *Balanus improvisus*, but the first shows slight radial thickenings in the calcareous base. These are not curved, however, but straight or nearly so. It is therefore possible that a difference in the habit of growth exists between the various species.

Moore (1935) suggested that the primary orientation, both of *B. improvisus* and of *B. balanoides*, was influenced by water currents, and he inferred that the cyprid attached by its antennules, settled with its anterior end facing and its posterior end trailing passively in the current, as shown in Fig. 4*a*. Barnes *et al.* (1951), however, found that under natural conditions the influence of water currents did not appear to be significant. They proved that the initial orientation of both species referred to by Moore and also of several others, coincided with that of the incident light. These conclusions were in accord with those of Hiro (1939), McDougall (1943) and Pyefinch (1948). Unfortunately, Moore does not record the lighting conditions under which his observations were made.

The present paper describes the relation between directly observed changes of orientation, the twist of the radial canals, and the direction of prevailing water currents.

TERMS AND CONVENTIONS

Before giving an account of changes in orientation during growth of barnacles belonging to the *B. improvisus* group, it is desirable to establish conventions of sign to describe the rotation of the axis of the opercular valves and the twist of the radial canals of the basis.

The tergal (carinal) end of the barnacle will be taken as the forward end in measuring orientations, since this coincides with the originally anterior end of the cyprid. As in earlier publications, the orientation of a given individual will be described by the angle ϕ between a reference (zero) axis and the rostro-carinal axis of the barnacle. ϕ will be assumed to run from 0 to 180° in the clockwise and from -0 to $-180°$ in the anti-clockwise sense from the zero axis, on the assumption that the barnacle is viewed from above. Any change in orientation $\Delta\phi = \phi_2 - \phi_1$ will be positive if rotation is clockwise, and negative if anti-clockwise. $\Delta\phi$ will be called the angle of rotation.

Fig. 1 illustrates two bases viewed from above in which the canals have (*a*) a dextral, and (*b*) a sinistral twist. A line drawn, making a tangent to a radial canal at its origin, such as *OA*, *OB*, represents the direction in which the canal would have grown had there been no torsion. The actual position of the extremity of the radial canal is at *A′* and *B′*. The angles *AOA′*, *BOB′* therefore indicate the probable twist of the basal margin during growth. This angle will be called the angle of torsion $\Delta\psi$, and will observe the same convention as the angle of rotation $\Delta\phi$, a dextral or clockwise torsion being regarded as positive. It will be obvious that if the basis is viewed from below, as for example through a glass panel, its torsion will be apparently reversed.

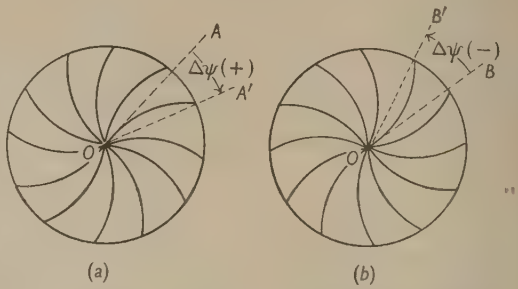


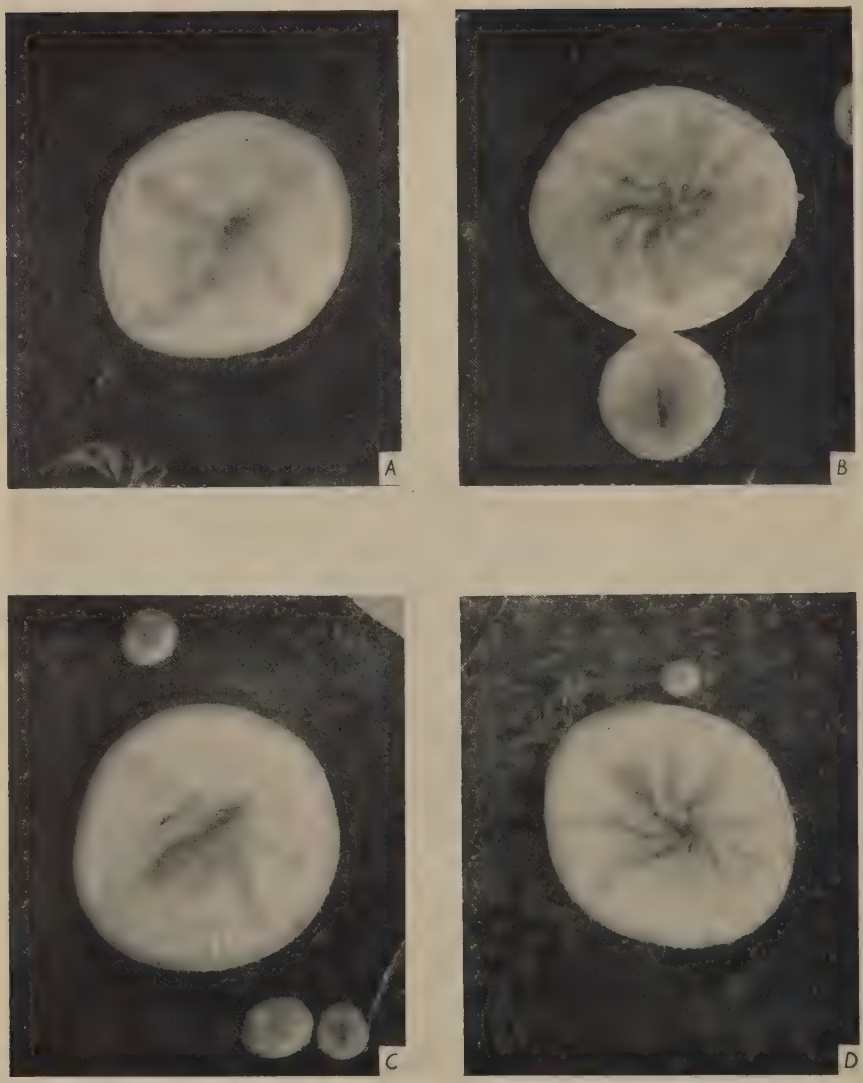
Fig. 1. Angles of torsion in (*a*) a dextral and (*b*) a sinistral individual as estimated from the twist in the radial canals.

ROTATION IN *BALANUS IMPROVISUS*

In order to investigate whether rotation occurred in *B. improvisus*, and whether it could be related to the observed twist in the radial canals, a late settlement of this species (together with a few *Elminius modestus*) was obtained on rectangular glass panels immersed in the River Mersey at Pierhead, Liverpool, between 20 September and 20 December 1951. These panels were transferred to Menai Bridge pier and re-established themselves over winter. Though *B. improvisus* did not grow appreciably it was easily distinguished the following year from *Elminius*, which had settled in approximately equal density. This procedure was necessary because *Balanus improvisus* is an estuarine form which is uncommon in the Menai Straits.

Fig. 2. Graduated eyepiece scale used as a goniometer.

The orientations were measured individually with reference to the long axis of the glass panels, using a low-power binocular microscope fitted with a scale eyepiece. The eyepiece was marked with a white spot corresponding to the direction of the linear markings of the eyepiece scale, and a protractor scale in a position corresponding with the axis of the plate was fixed below the eyepiece (Fig. 2). In operation the eyepiece scale was aligned with the axis of the barnacle and the white spot on the eyepiece then marked the correct orientation when viewed against the protractor scale. This arrangement made rapid readings possible to an accuracy of $\pm 2°$. A photograph was made of each plate before recording orientations, so that the individuals could be numbered on a rough print for subsequent identification.



Photographs of the underside of bases of *B. improvisus* showing radial canals taken through a glass plate, *A*, sinistral torsion; *B*, dextral torsion; *C*, absence of torsion; *D*, variable torsion. Note that when viewed from below the sign of the angle of torsion is apparently reversed.

By this means orientations measured on 6 March 1952 were compared with measurements of the same individuals made on 1 May 1952. During the interval rapid growth had taken place, and many individuals were mature and bore fully developed egg masses. The plates, after being examined from above on 1 May 1952, were then reversed and the radial canals examined under the binocular with low side lighting to render them clearly visible. In this experiment individuals were obtained showing sinistral (Pl. 6*A*) and dextral (*B*) twists, or direct radial growth without torsion (*C*). In some individuals a reversed twist was observed in the growth of the canals (*D*). Owing to irregular growth, the twist in the canals was not normally uniform over the whole circumference (i.e. $\Delta\psi$ was variable along different radii). It was not possible therefore to assign a definite value for $\Delta\psi$ to each individual except by averaging several measurements. This operation, if performed with the eyepiece scale, became tedious and did not give results showing any greater consistency than could be obtained by eye using an unscaled eyepiece. The latter method was therefore

Table 1. *Relation between twist of radial canals* ($\Delta\psi$) *and rotation of rostro-carinal axis* ($\Delta\phi$) *in* Balanus improvisus

Range of ψ	No. examined	Mean value for $\Delta\psi$ (°)	Mean value for $\Delta\phi$ (°)
Dextral			
+40° to +31°	1	+35	+30
+30° to +21°	3	+27	+22
+20° to +11°	8	+17	+10
+10° to + 1°	18	+ 7	+ 6
No obvious twist	17	0	+ 3
Sinistral			
− 1° to −10°	11	− 7	− 9
−11° to −20°	2	−17	−15
−21° to −30°	1	−25	−17
−31° to −40°	0	—	—
Total	61		

adopted to estimate $\Delta\psi$. Another feature which caused measurements of $\Delta\psi$ to be less reliable than those of $\Delta\phi$ was the occurrence in some individuals of changes in the direction of twist of the canals during growth (Pl. 6*D*), or of canals which were strongly twisted near the centre but had later straightened out. In these cases it was not always clear what to assume as the initial direction of the canals appropriate to the first examination of 6 March 1952, when the individuals were so small that the canals were not clearly visible.

Table 1 summarizes the results, which are grouped according to the observed twist of the radial canals. There is no doubt that some individuals exhibit considerable rotation, the maximum value for $\Delta\phi$ in this series being of the order of +40°. The majority showed only slight rotation, or sometimes if we may judge by the radial canals, a variable rotation. The correlation between the twist of the radial canals and the observed rotation is very close, and establishes that the form of these canals may be employed to trace changes in the rostro-carinal axis. The small differences between $\Delta\psi$ and $\Delta\phi$ may be ascribed partly to irregular growth noted above, and perhaps to a small degree of torsion present in the parietes.

TORSION IN *BALANUS AMPHITRITE*

A settlement of *B. amphitrite* was obtained on glass panels in the cooling pond of Southwick power station near Shoreham Harbour, where it settles in abundance during the summer months (Bishop 1950, Crisp & Molesworth 1951). As the panels were suspended vertically from the sides of the pond and the light fell mainly from above, there resulted on settlement a strong vertical orientation of the young barnacles. They were transferred to Brixham Harbour, photographed and numbered, those which were not initially pointing upwards within 10° of the vertical axis being ignored. The panel was removed several months later and the orientations of the main axis, together with twists of the radial canals, were measured. Unfortunately there was considerable mortality, due probably to the change in temperature of the environment. The results are shown in Table 2. These results were subject to greater error than those of the previously described experiment, not only because fewer individual observations were made, but also because, instead of making initial measurements of the orientation of each barnacle, the population was crudely selected for those which had an orientation lying between $0 \pm 10°$. Thus the subsequently recorded values of ϕ approximated to the angles of rotation $\Delta\phi$. By grouping the observations as a contingency table, it

Table 2. *Contingency table showing correlation between the twist of the radial canals $\Delta\psi$ and the approximate angle of rotation $\Delta\phi$ in* Balanus amphitrite

	$\Delta\psi > +40°$	$+40°$ to $+15°$	$+15°$ to $-15°$	$-40°$ to $-15°$	$< -40°$	Total
$\Delta\phi > +40°$	2	1	2	0	0	5
$+40°$ to $+15°$	1	3	1	0	0	5
$+15°$ to $-15°$	0	0	3	0	1	4
$-15°$ to $-40°$	0	1	7	11	0	19
$< -40°$	0	0	4	2	3	9
Total	3	5	17	13	4	42

becomes clear that in this species too a correlation, both in magnitude and in sign, exists between the orientation acquired by rotation and the angle of torsion of the canals in the basis.

RELATION BETWEEN TORSION AND WATER MOVEMENTS

In the experiments described both sinistral and dextral torsions have been observed. Although there was no great regularity in behaviour, in general one or the other predominated on any one plate. Observations on torsion in naturally occurring populations showed the same phenomenon; taking a number of samples over a wide area the total numbers of dextral and sinistral individuals were about equal, but within small groups of individuals either dextral or sinistral twists might appear to predominate to a degree greater than could be attributed to mere chance. The distribution of dextral and sinistral individuals is therefore contagious rather than random. This type of distribution suggested that an external factor was operating, rather than that the twists were due to an innate tendency, for the population must be derived from larvae of diverse origin. The external factor appears to be one which is not constant even over a small area, but varies a good deal from point to point, and judging from

the individuals with reversed torsion, also occasionally from time to time. The most likely factor which might operate in this way is the eddying of water past the substratum.

Owing to the variation of the tidal streams, there is little possibility of correlating torsion with the direction of water currents under entirely natural conditions. However, if a floating structure is moored at one end and thereby allowed to swing with the tide, its surface is exposed to fluctuating but unidirectional currents. A wooden pontoon at the mouth of the River Conway, which had been continuously moored in this way, was beached and found to bear on its vertical sides a settlement of *B. improvisus* with a few *B. crenatus*. Observations were made on the orientation and torsion of the individuals growing on it; the change in orientation was estimated by the twist of the radial canals on the assumption that the correlation previously noted between rotation and torsion was generally true.

The results shown in Table 3 were obtained from barnacles growing amidships on the vertical sides of the pontoon. In considering the results, it should be noted that to an observer facing the port side the current flow is from left to right; facing the

Table 3. *Torsion in* Balanus improvisus *exposed to unidirectional currents*

Original position corrected for torsion, $\phi - \Delta\psi = \phi_0$	Port side (current left to right)				Starboard side (current right to left)			
	No. dextral	No. sinistral	No. neutral	Mean $\Delta\psi$	No. dextral	No. sinistral	No. neutral	Mean $\Delta\psi$
Barnacles pointing upwards, $90° > \phi_0 > -90°$	13	1	9	+10·1	1	18	6	−23·6
Barnacles pointing downwards, $180° > \phi_0 > 90°$, $-180° < \phi_0 < -90°$	1	3	1	−8·0	2	0	1	+15·0

starboard side the flow is from right to left. Before entering the results in the table, the orientations (ϕ) measured from the vertical were corrected by the estimated torsion ($\Delta\psi$) to give a more accurate value for the original position (ϕ_0) at settlement. The correction was small, usually less than 20°. It will first be noticed that the majority of individuals were orientated upwards with the cirri beating down; on the port side 23 and on the starboard 25 out of 28 were orientated between 0 and $\pm 90°$. The primary orientation may therefore reasonably be ascribed to the light gradient as in previous observations, since the direction of the light may be assumed to be from above.

The torsion of those individuals which pointed typically upwards, $90° > \phi_0 > -90°$, is given in the first row of the table and shows a striking correlation with the current; nearly every individual had rotated in the direction towards which the current was flowing so that the cirri tended to beat into the current. The barnacles pointing downwards showed a similar tendency, although the samples consisted of rather small numbers. By making $\Delta\psi$ positive when the barnacle rotated to fish into the current, all the results of Table 3 could be grouped to show the relation between $\Delta\psi$ and the original direction of the barnacle in relation to the current. The result is shown in Fig. 3, the mean $\Delta\psi$ being plotted against the angle between the orientation of the barnacle and the horizontal ($\phi_0 \sim \pm 90°$). Although the errors associated with each

point are too great to allow a curve to be drawn expressing the relationship, it is clear that the greater the deviation of the barnacle axis from the direction of the current the greater the observed torsion.

Measurements of torsion were also carried out where the flow past the pontoon could not so readily be predicted. On the starboard side well forward, close to the scow-end, the majority of barnacles pointed upwards and possessed a typical negative

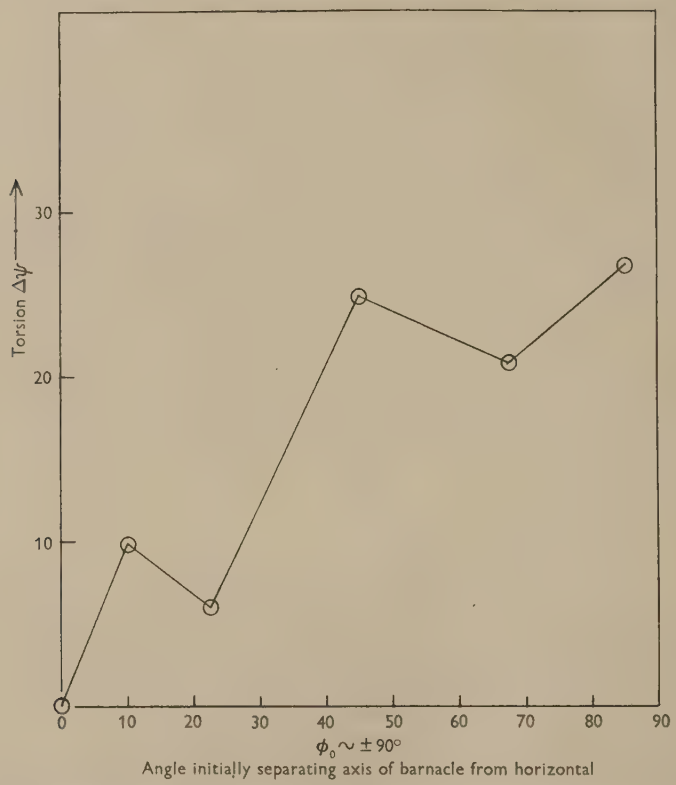


Fig. 3. Relation between torsion and deviation of the barnacle axis from the direction of flow of the current (from grouped data).

torsion; they differed from those further back however in showing rather less twist ($\Delta\psi = -6°$ from 18 individuals). The flow here would be expected to have an upward as well as a horizontal component, due to the water forced down by the scow-end rising on either side. This would reduce the tendency to rotate by diminishing the angle between the barnacle axis and line of flow. At the back of the raft which was vertical, the few individuals available tended to rotate so that the cirri beat upwards, for those with positive angles to the vertical axis had rotated to the right; those with negative angles, to the left. This would accord with a downward eddy at the stern.

ECOLOGICAL SIGNIFICANCE OF TORSION

The importance of the direction of water currents in relation to beat of cirri in *B. balanoides* and *B. improvisus* has been stressed by Moore (1935), who states that in a stream of water the cirri often remain motionless, extended in the fishing position. A similar response to violent streams of water was noted in *Chthamalus stellatus* under natural conditions of wave swash (Crisp 1950). Whether the cirri function primarily as feeding organs or to promote respiratory exchange, it can scarcely be doubted that they will work with greater economy if they are able to beat against the current. Moore, taking into account the two-directional character of tidal streams, considered that alignment across the current would be advantageous by allowing the barnacle to make use of the

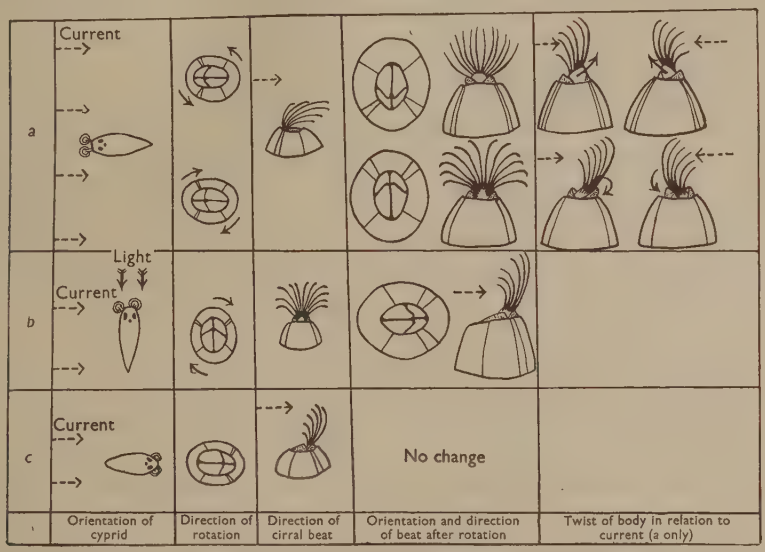


Fig. 4. *a*, orientation by current, effect of 90° rotation, and consequent body twist to bring the cirral beat into the current, as postulated by Moore; *b*, orientation in response to light and rotation produced by current as described in these observations; *c*, primary orientation in relation to currents in *Balanus balanoides* and *Elminius modestus* and consequent cirral beat, as considered to occur in absence of effective light stimulus.

flow in both directions. His conclusion that a rotation took place in the manner illustrated in Fig. 4*a* was not however based on sufficient evidence. He did not follow the change of orientation in individuals but only recorded mean differences between age-groups, which might have settled under different conditions.

The evidence presented here indicates, on the contrary, that orientation changes shown by barnacles like *Balanus improvisus*, are in such a direction as to rotate the animal to bring the cirri against the prevailing current, as in Fig. 4*b*, rather than at right angles to it; moreover, the greater the initial deviation of the animal from the current axis, the greater the observed tendency to twist. This mechanism would be an obvious advantage to a barnacle living in a unidirectional tideway. It would appear at first sight to be of little value in the normal marine environment, but it is the

exception, rather than the rule, for tidal streams to show an evenly balanced flow of simple harmonic type, particularly near coastal irregularities and in estuaries. Estuaries in particular are subject to asymmetrical tides, there being relatively short periods of flood and long periods of ebb, and the ebb is further augmented by any residual flow of freshwater. Furthermore, it is not unusual also to find pockets of predominantly unidirectional flow in estuaries where the normally opposing tidal streams flow on a slightly different course, so that in certain places the current is replaced at the turn of the tide by a back eddy. Conditions of this kind have been observed by the author in the River Dart at Greenway, and in the Menai Straits. An adaptation enabling a barnacle to re-orientate itself to currents might therefore be advantageous in estuaries, especially in the sublittoral zone where wave action has negligible effects. It is probably significant that the two barnacles in which rotation has been definitely shown to occur are predominantly estuarine and sublittoral, *B. improvisus* in particular being rarely found elsewhere. Other species known to show similar twists in the radial canals and therefore probably able to rotate, are *B. perforatus* and *B. eberneus*, both of which are forms favouring sheltered conditions, and well able to withstand the typical estuarine fluctuations of salinity (Norris & Crisp 1953). On the other hand, barnacles which occur higher up the intertidal zone and are subjected to irregular wave swash (e.g. *B. balanoides* and *Chthamalus stellatus*) and also those from deeper water offshore (e.g. *Balanus crenatus*, *B. porcatus* and *B. hameri*), show little evidence of torsion. *Elminius modestus*, which is both intertidal and typically estuarine, has likewise no ability to change its orientation after settlement.

PRIMARY ORIENTATION IN RELATION TO WATER CURRENTS

Moore (1935) implies that the initial orientation induced by water currents is mechanical, the cyprid holding on by the antennules with the body swept behind by the current (Fig. 4*a*). This orientation he rightly points out would be disadvantageous (1935, p. 298): 'After metamorphosis of a cypris larva in a current of water, the newly formed barnacle would be orientated with its cirri facing down the current of water in a position most disadvantageous for capturing food, and rotation would clearly be desirable.'

However, he offers only indirect evidence that the cyprids are initially orientated by the current in this way. It is now clear that orientation due to daylight normally takes precedence over any effect due to water current. Moreover, direct observations leading to the same conclusion have been carried out on the cyprids of *Elminius modestus*, *Balanus balanoides* and *B. crenatus*, by allowing them to attach to the inner surface of long narrow glass tubes and exposing them to currents of water. These currents established a considerable velocity gradient at the boundary (rate of shear) of 100 $sec.^{-1}$, calculated from Poiseuille's equation (1846). Yet cyprids of all three species were observed to possess sufficient strength to rotate the body about the antennules in various positions following the direction of the light, and even to point the tail upstream and walk along in the same direction as the current. This was admittedly the most insecure position, for it was the one most frequently terminated by swimming; but even at 1000 $sec.^{-1}$ cyprids of *Elminius modestus* could still migrate against or across the current, although unable to maintain their hold with their posterior end

directed upstream. A shear of 100 sec.$^{-1}$ corresponds to a velocity of 2 knots at a distance of 1 cm. from surface, a condition as rigorous as would be anticipated in a tideway. It is not possible to relate these observations to those of previous investigators who have studied settlement in relation to water currents, as these observers have considered only the relation between attachment and the rate of flow of the main body of water past the surface (Smith 1946; Doochin & Smith 1951). It is the rate of shear at the boundary where settlement is taking place which most nearly describes settling conditions for small larvae, and this can only be related to the external flow under specified conditions.

It therefore appears probable that the cyprid possesses the physical ability to orientate in any position when setting in a water current, although in setting against the current it would be mechanically more stable. If this is true, Moore's argument might be reversed; a cyprid settled with its posterior end facing the current as in Fig. 4*c* would have an obvious advantage.

Preliminary observations, limited to *Balanus balanoides* and *Elminius modestus*, have now been made on the dark parts of the hulls of several craft known to have been moored at one end and subjected to unidirectional flow. These observations will be published in detail later, but the orientations of adult barnacles indicate that when directional light is at a minimum, the cyprids do indeed orientate in this way, although the stimulus is a weak one, since photo-orientation takes precedence over it. If this reaction can be confirmed by direct observation on the cypris larva, it will provide a remarkable example of a response which, though immediately inconvenient or possibly disadvantageous, confers benefit to the individual after metamorphosis.

Rotation therefore appears normally to be an adaptation to bring the barnacle from its original position orientated towards the light or in response to surface irregularities, to a position with the cirri beating into the current. In the absence of other stimuli, however, it would serve as a double assurance, reinforcing a primary response orientating the cyprid to the current prevailing at the time of setting.

TORSION AND GROWTH

The shape of an acorn barnacle, particularly one with a calcareous basis, does not allow of many possible modes of accretional growth. If there is no extensive resorption of the shell, and on the assumption that a conical shape is retained, the zone of growth must be mainly at the basal perimeter. Where new growth is distinguishable from the old, it is always in fact observed at the basal margin and at the lateral junction of the compartments (Darwin 1854). Parke & Moore (1935) refer to the manifestation of this basal growth due to the darkening of older parts of the shell by symbiotic algae. At the base additional shell can be considered to be produced in the following directions (Fig. 5):

(*a*) Radially, forcing the growth zone of the basis outwards along *OR*.

(*b*) Tangentially maintaining the perimeter by growth along *RP*, AP^1, etc.

(*c*) Apically or columnar growth, increasing the height of the shell *RA*, PP^1, etc.

(*d*) Abapically, tending to grow into the substratum along *RB*.

The abapical growth is normally zero owing to the resistance of the substratum, but the tendency is there, for irregularities of the surface are not overgrown but are filled

up, whilst the growing edge tends to plough under any loose or soft obstruction such as a paint film. If growth in any other direction is resisted, the amount of growth is similarly reduced; for example radial growth is inhibited when the barnacle is in contact with adjacent individuals, leading to the typically columnar form. Thus the amount of growth taking place may be controlled by mechanical forces—in other words the animal's growth shows plasticity, as Barnes & Powell (1950) concluded from observations on growth forms of *Balanus crenatus*. This plasticity is clearly of importance in many respects; it allows the animal to key itself into irregularities, and it may well be the mechanism by which components of normal unrestricted growth are correlated.

If this plasticity of growth can be evoked by fairly small resultant forces acting over a long period, a simple explanation of torsion may be advanced. The animal is known to rotate the body in the mantle cavity by means of muscles which are inserted in the basis and hence adhere to the substratum. The rotation is such that the cirri spread

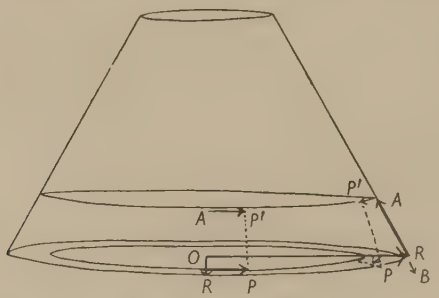


Fig. 5. Diagram showing the directions of growth of an acorn barnacle, assumed to approximate to a truncated cone continuously added to at the basal perimeter.

out at right angles to the prevailing water current, as shown at the right-hand side of Fig. 4*a*. In the process the attachments of the body to the shell presumably transmit some degree of strain to the parietes in the direction of the twisting of the body. If additional growth takes place more readily in the direction of tension, and less in the direction of compression, each element of the perimeter will add rather more substance to the side favoured by the twist, and will therefore cause the animal to rotate in the preferred direction during growth.

It is also possible that different species exhibit intrinsic differences in their habit of growth which may favour or preclude torsion. In some there may be a tendency for the rate of peripheral growth to exceed radial growth; this would produce in the bases a state of compression tangentially and of tension along the radii (Fig. 6*a*). On the other hand, if radial growth predominates (Fig. 6*b*) there will be tension around the periphery and radial compression. Clearly the former mode of growth will promote a ribbed or crenated border, and a thin flat basis with straight growth-lines radiating from the centre. The latter condition, on the other hand, would result in a smooth border but with a tendency for the basis to be folded or channelled, probably with more and more such folds appearing as the basis increased in size. Moreover, under these conditions the lines of growth in the basis would be more easily distorted into

a spiral, for if the radial canals were to become spiral and cut the circumference, say at an angle of 30° instead of 90°, their rate of linear growth could then be twice as great as that of the true radius, and so be consistent with a deficient rate of growth at the circumference. In other words, a tendency for the radial growth to exceed peripheral growth would make torsion easier, while excessive peripheral growth should tend to reduce any tendency to torsion.

These considerations are on the whole borne out by the limited number of species in which evidence for torsion has been sought. Both those which have been shown to exhibit torsion have smooth margins and nearly circular perimeters, viz. *B. improvisus*, *B. amphitrite*. *B. perforatus* and, I believe, *B. eburneus* also exhibit twisted radial canals and presumably can rotate during growth; they too are smooth unless eroded. On the other hand, *B. balanoides*, *Chthamalus stellatus*, and *Elminius modestus*, which do not show torsion, typically have folded or wrinkled margins. *Balanas porcatus*, *B. crenatus*,

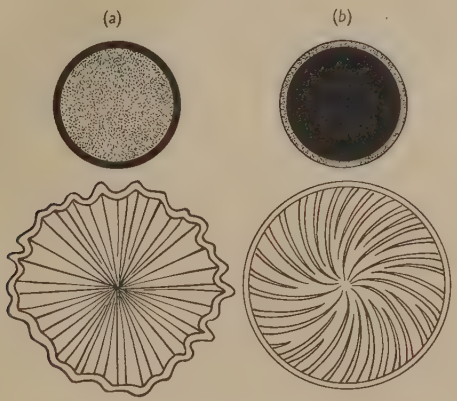


Fig. 6. Effect of differential growth-rates of the basal perimeter and radii in an acorn barnacle. *a*, growth at the perimeter exceeding that of the basis, and consequent change of shape; *b*, radial growth exceeding peripheral growth, and consequent twisting of the basis. Black regions indicate compression, stippled areas, tension.

and *B. hameri* have radial growth-lines which are almost or quite straight, so these species may be presumed not to rotate. *B. porcatus* has folded margins, *B. crenatus* is sometimes folded and *B. hameri*, though smooth, has a peculiar shape, which suggests that its growth is not confined to the basal margin to such an extent as in related barnacles. It appears that species which have folded margins do not rotate, and that those which do rotate have smooth margins. It remains to be seen whether this correlation will prove to be sufficiently general to support the theory of growth which has been tentatively advanced.

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SUMMARY

1. Both *Balanus improvisus* and *B. amphitrite* are capable of rotation of the rostro-carinal axis during growth.

2. The twist which may be observed in the radial canals offers a reliable guide to the direction and magnitude of this rotation.

3. Rotation may be to the right, to the left, or may vary in direction during growth. Often no rotation occurs and the radial canals are straight.

4. Rotation is related to the direction of the prevailing water current, and is in such a direction as to cause the cirri to beat into the current.

5. Re-orientation of a barnacle in this way may be of adaptive value under estuarine or coastal conditions where tidal flow may be predominantly in one direction and where wave action is negligible.

6. Primary orientation in daylight is determined by the direction of the resultant light intensity, but if there is no light gradient, there is probably a direct reaction to water currents at the time of settlement. The latter causes the cypris larvae to settle pointing downstream and confers a favourable orientation on the adult.

7. It is suggested that rotation follows from the twisting of the body in relation to the shell. This twist brings the cirri to beat into the current, and the predominant feeding position influences a plastic region of growth by setting up mechanical strain. Ability to rotate may vary according to the natural strains arising through differences of growth rate between the base and its periphery.

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POPULATION DENSITY IN ADULT DRAGONFLIES (ODONATA-ANISOPTERA)

By N. W. MOORE

*Department of Zoology, University of Bristol**

(With 7 Figures in the Text)

INTRODUCTION

Few invertebrates provide better opportunities than dragonflies for quantitative population study. They are large, diurnal and predatory. Their normal densities of population, like those of other carnivores of similar size, are comparatively low. Most British species can be identified in the field at a range of several feet. Altogether it is surprising that no published account of a population study of Anisoptera exists, as far as the writer is aware. It is owing to their size and habits that accurate censuses of dragonflies in quite large areas can be made without resort to sampling methods. Direct counts of all the individuals seen in the areas studied form the basis of the present work. The entire study was a general one, but maximum density and its bearing on interspecific relationships are the only aspects dealt with fully here.

Dragonflies roost in vegetation away from water. During the morning mature males fly to water and remain there till the afternoon. Mature females pay much shorter visits to water during the day. Immature imagines keep away from water throughout the day. A census of dragonflies when they are dispersed in the roosting area is clearly impossible; but counting them when they are concentrated by water was found to be a relatively easy matter. This was done throughout the investigation. Two aspects of maximal density by water were studied: the first part of this paper is concerned with the daily maximum, the second with seasonal maxima.

The areas studied during four consecutive summers were:

(1) A half mile stretch of the drainage ditch known as the Portbury River, where it forms the boundary between the parishes of Weston-in-Gordano and Walton-in-Gordano, near Portishead, Somerset (Nat. grid ref. 31/451735).

(2) The pond in Old Sneed Park, Stoke Bishop, Bristol (Nat. grid ref. 31/555755).

The valley through which the Portbury River flows lies between the Bristol Channel and the North Somerset 'moors'. It is separated from both by limestone hills of about 300 ft. high. The floor of the valley is flat. The upper (south-western) part, in which the census area lies, consists mainly of fen, carr, and rough pasture; the fields are separated by ditches. The lower part consists of pasture on clay alluvium; here the fields are separated by hedges. The fall of the river from source to sea is about 25 ft. in about 5 miles; the rate of flow is therefore slight and varied in the census area from 0 to about 0·8 ft./sec. The width of the river in the census area was 7 ft. at its narrowest, 16 ft. at its broadest. The depth varied seasonally from a few inches to about 2 ft. At times much of the valley was flooded. *Elodea* was the dominant submerged plant. The most abundant partly emersed plant was *Alisma plantago-aquatica* L. *Phragmites*

* Now at The Nature Conservancy, Furzebrook Research Station, Wareham, Dorset.

communis Trin., *Hippuris vulgaris* L. and *Equisetum* sp. were locally abundant. For the topography of the area see Fig. 1.

The pond at Stoke Bishop was formed originally by damming a steep valley in an old deer park. It is about 140 yd. long and about 40 yd. wide at its broadest. It is surrounded by trees and bushes except for about 50 yd. of its north-western side. In summer most of the surface is covered with the leaves of *Lemna* and *Nuphar*. It is much more sheltered than the Portbury River, but does not get early sun.

Some counts were also made at a small cattle pond by Round Hill Clump, Abbots Leigh, Somerset. It is about 9 yd. broad, 10–15 yd. long. The west side is partly sheltered by a thorn hedge. It is covered with duckweed for much of the summer.

The visits made to the census areas are shown in Table 1. The records for Portbury River and Stoke Bishop are much more complete for 1951 and 1952 than for 1949

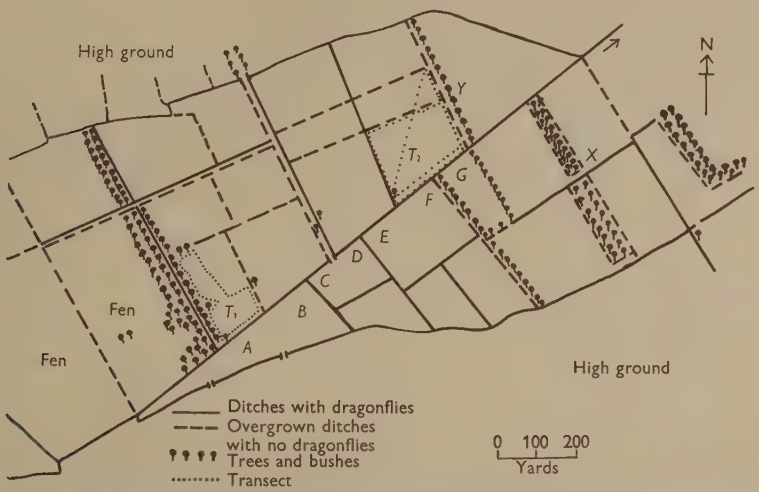

Fig. 1. Sketch-map of the Portbury River census area showing the positions of its sections and of the transects in the roosting area. For details see text.

and 1950. No records were made at the beginning of the 1949 season at Portbury, nor from midsummer to mid-autumn in 1950. Census counts made there in October 1950 are not comparable because the area had been flooded since early September. At Stoke Bishop pond no counts were made after 9 July in 1949, nor between 6 July and 10 October in 1950.

The species studied were:

Brachytron pratense (Müller)
**Aeshna cyanea* (Müller)
**Anax imperator* Leach
†*Orthetrum cancellatum* (L.)
†*Libellula quadrimaculata* L.
**L. depressa* L.
**Sympetrum striolatum striolatum* (Charpentier)

Other species recorded from the census areas were:

†*Aeshna grandis* (L.)
A. juncea (L.)
A. mixta Latreille
Orthetrum coerulescens (Fabricius)
†*Sympetrum sanguineum* (Müller)

All were recorded from the Portbury River. All bred there regularly except for *Aeschna grandis*, *A. mixta*, *Orthetrum coerulescens*, *Sympetrum sanguineum*.

Those marked * occurred regularly at the Stoke Bishop pond. Those marked † occurred occasionally at the Stoke Bishop pond.

METHODS

Male dragonflies remain in rather limited areas when by water. Some of their time is spent perched on emergent water plants or on the bank and some in flight in search of food and mates (Aeshnines perch little, Libellulines, especially *Sympetrum*, perch often). It is difficult to drive them from their beats. Flying dragonflies are easily seen, especially against sky or water, so it is easy to count them; but a motionless dragonfly, however large, is easily overlooked. To make an accurate count of male dragonflies by water all must be made to fly. It is because this is so easily done that accurate counts can be made. The range of vision of dragonflies is good—they react to movements

Table 1. *The numbers of days in each month on which counts were made at the census areas*

		May	June	July	Aug.	Sept.	Oct.	Nov.	Total counts
Portbury River	1949	0	7	2	1	1	3	1	
	1950	3	5	0	0	0	2	0	164
	1951	2	3	8	6	6	4	2	
	1952	5	6	2	2	4	4	1	
Stoke Bishop pond	1949	1	2	2	0	0	0	0	
	1950	0	6	1	0	0	2	1	254
	1951	1	2	3	4	10	8	1	
	1952	3	7	3	2	7	4	1	
Abbots Leigh pond	1952	1	3	0	0	5	2	0	52

made over 30 ft. away. They react to all quick movement by flying, because the first stage of their feeding, reproductive, and escape activities is flight. Therefore by walking fairly quickly along a stream or by the edge of a pond an observer can quite easily put up all the dragonflies present and record them. He must make sudden movements; the writer waved a large stick over the water as he walked. Since females by water are nearly always mating or laying eggs they are also easily counted.

Inaccuracies in the direct count are of two kinds; those of identification and those of counting. The differences between the species studied are very marked, and since the writer has been acquainted with all the species for over ten years, errors due to faulty identification were almost certainly negligible. The greatest accuracy in counting must be obtained when most individual dragonflies are perched initially, but all fly when disturbed. Some inaccuracies undoubtedly occur when many dragonflies are on the wing at once, and when they do not fly on being disturbed. The first situation occurs most frequently in the morning on very hot days, and the second when there is a drop in temperature after the dragonflies have gone to water. It was not possible to estimate the degree of accuracy of the counts, but this was undoubtedly higher than any which could be got by other methods, including that of marking and recapture. (This technique is not suitable for Anisoptera—their population densities are too low,

the time taken to capture them too great. It has been used with success for the Zygopteran *Pyrrhosoma* (Corbet 1952).) It is probable that counts of dragonflies can be unusually accurate.

In this paper an attempt has been made to correlate dragonfly behaviour with temperature fluctuations of the environment. Since dragonflies perch and fly in the sun whenever possible, they are affected not only by air temperature and air movement but by radiation as well. Therefore shade temperatures are largely irrelevant. A rough indication of the fluctuations of the effective temperature environment was obtained by fixing a thermometer with the bulb painted white in the sun in the air about 3–4 ft. above the ground. When constant readings were obtained they were recorded. Temperatures got in this way are called 'exposed thermometer temperatures' throughout this paper.

OBSERVATIONS

(*a*) *The daily rhythm of activity and the effects of weather upon it*

In order to discover the occasions when dragonfly populations were most dense, it was necessary to know the normal daily activity rhythms of the species studied. This was achieved by making counts at different times of the day, both total counts by water and sample counts in the neighbouring roosting area. It appeared that the presence or absence of dragonflies by water was connected with variations in atmospheric temperature, both with time of day and with weather. Therefore correlation of behaviour with conditions due solely to time of day could only be obtained when weather was uniform. The data summarized in Tables 2 and 3 were obtained on days with little or no cloud, and with very little wind.

Table 2. *Time of highest densities of dragonflies by water, when weather was favourable*

	Days on which the count nearest noon		
	Was highest or equal highest	Was not highest or equal highest	Census figures when the noon count was not the highest; the first figure is the noon count
MALES			
Brachytron pratense	11 (6)	4 (2)	3/6, 9/11, 2/3, 1/2
Aeshna cyanea	9 (0)	10 (0)	3/5, 2/4, 2/3, 1/2, 1/2, 1/2, 1/2, 0/1, 0/1, 0/1
Anax imperator	15 (4)	2 (2)	7/8, 1/2
Libellula depressa	13 (5)	7 (2)	9/11, 3/4, 2/3, 2/3, 1/2, 0/1, 0/1
L. quadrimaculata	17 (16)	4 (2)	7/11, 11/13, 2/3, 2/3
Orthetrum cancellatum	13 (10)	2 (2)	7/9, 5/7
Sympetrum striolatum	25 (23)	6 (6)	14/36, 11/21, 15/20, 12/15, 14/15, 6/7
FEMALES			
Brachytron pratense	4 (0)	1 (0)	0/3
Aeshna cyanea	5 (0)	5 (0)	1/2, 0/1, 0/1, 0/1, 0/1
Anax imperator	9 (2)	2 (0)	0/1, 0/1
Libellula depressa	6 (0)	2 (0)	0/2, 0/1
L. quadrimaculata	6 (0)	4 (0)	0/1, 0/1, 0/1, 0/1
Orthetrum cancellatum	5 (0)	5 (0)	0/2, 0/2, 0/2, 0/1, 0/1
Sympetrum striolatum	19 (9)	9 (4)	4/11, 4/10, 0/3, 0/3, 7/9, 2/4, 0/2, 1/2, 0/1

Figures in brackets give numbers of days when highest count was of four or more insects.

Counts of *Brachytron pratense*, *Anax imperator*, *Libellula depressa*, *L. quadrimaculata* and *Orthetrum cancellatum* were all, or nearly all, made at the census area by the Portbury River, those of *Aeshna cyanea* mainly at Stoke Bishop pond, those of *Sympetrum striolatum* at both localities. At Portbury River one count on each day was made within 2½ hr. of noon (generally at or very near noon). The count with which this is compared in Table 2 was never more than 3 hr. before or after it. Usually each count took from 15 to 30 min. to make. At Stoke Bishop pond counts were made more frequently.

Two conclusions are drawn from the data summarized in Tables 2 and 3. In all species except *Aeshna cyanea* the count nearest noon usually gave the highest or equal highest density of male dragonflies recorded for that day. Unlike those of other species, *A. cyanea* males often leave the water and return to it later in the day; although they show roughly the same rhythm as those of the other species studied, their density at noon is often not the highest of the day.

Table 3. *Sex ratio in populations of dragonflies by water, when weather was favourable*

	Total records of males	Total records of females	Number of counts when: Males > females	Number of counts when: Females > males
Brachytron pratense	132	12	29	0
Aeshna cyanea	111	19	54	9 (sex ratio 0:1 in each case)
Anax imperator	121	28	35	2 (sex ratio 3:4 and 0:1)
Libellula depressa	178	13	36	0
L. quadrimaculata	710	16	53	0
Orthetrum cancellatum	322	16	37	0
Sympetrum striolatum	1318	566	117	0

N.B. Exact specific differences in behaviour cannot be deduced from the data above.

Usually the density nearest noon was considerably higher than those of mid-morning and mid-afternoon. When the highest density did not occur at noon it usually differed from the noon (or near noon) density by very little—1 to 4 insects for all species other than *Sympetrum striolatum*. In this species three important exceptions were recorded. On 20 July 1951, 36 males were counted at Portbury at about 1030 hr. G.M.T., and 14 at about 1200 hr. On 4 October 1951, 11 males were counted at noon at Stoke Bishop, 21 at 1245 hr. On 8 October 1952, 15 males were counted about 1210 at Portbury, 20 about 1240 hr. On both the October days temperatures were low; on 4 October 1951 the exposed thermometer temperature in the sun never rose above 17·5° C., and on 8 October 1952 never above 16·5° C. The delayed density peaks on these days were almost certainly attributable to low temperatures. No meteorological factor can be invoked to account for the record of 20 July 1951. The weather was ideal and the other species present showed normal noon peaks. The causes of this exceptional record are discussed on p. 358. It is concluded that the diurnal rhythm of *S. striolatum* does not differ from those of the majority of the other species studied; on fine days males are most frequent by water at noon.

Secondly, although on the whole female dragonflies appear to be more numerous at water at noon than at other times (Table 2) the number of females compared to

males on any one count is nearly always very small (Table 3). So either females are much less numerous than males, or they spend much less time by water than do males. The true sex ratio has been established for very few species, but in all the Anisoptera so far investigated it appears to be about 1:1 (Corbet 1952; Moore, unpublished). Also, continuous observation showed that individual females do in fact spend very little time by water; they come to mate and lay eggs, but they never feed there as do males. On 18 June 1949, a marked female, *Libellula depressa*, visited the Portbury River twice in one day, and oviposited on both occasions. This is probably exceptional, and may have been caused by disturbance due to marking on the first occasion. Whether females visit water every fine day is not known.

The length of the midday peak period for males was found to be variable. For example 4 male *L. quadrimaculata* were counted at 1000 hr. on 29 June 1950, and 15 at noon. But on 20 July 1951, 29 were counted at 1030 hr., and 30 at noon. Therefore the size of the noon population cannot be deduced from counts made at other times.

Fig. 2 illustrates the typical rise and fall in numbers of male dragonflies by water on fine days. At the Portbury River on 2 August 1951 the population at the noon peak consisted of 1 *Anax imperator*, 1 *Libellula depressa*, 13 *L. quadrimaculata*, 8 *Orthetrum cancellatum* and 29 *Sympetrum striolatum*. At Stoke Bishop pond on 18 September 1952 the population at the noon peak consisted of 15 *S. striolatum* and 2 *Aeshna cyanea*. Casual observation shows that weather affects the numbers of dragonflies present by water; on cold sunless days they are not found there at all. If morning sun is followed by cloud and cold, those by water can often be seen flying back to the roosting area much sooner than they would have done if the day had kept fine. It is clear that temperature and not the mere presence of the sun is the important factor, for if the sun's disappearance is not accompanied by an appreciable drop in temperature, as occurs on windless days in midsummer, the dragonflies remain by water. Also, on days when there is no cloud but a strong wind, dragonflies do not go to water but are to be found in the sheltered parts of the roosting area at noon. For example, between 1200 and 1248 hr. G.M.T. on 24 September 1951, 27 male and 7 female *Sympetrum striolatum* were counted on sheltered bushes, etc., away from the Portbury River, but by the water no dragonflies were seen at all. A very strong (at least force 5) south-westerly wind was blowing and the air temperature in exposed places in the sun was about 17·0° C. If the air is not warm the presence of dragonflies by water depends on the sun's appearance, for, like other insects, they are dependent on direct solar radiation (Parry 1951). Fig. 2*c* illustrates this. Although the exposed thermometer temperature remained much the same when the sun disappeared behind cloud, the insects left the water, and did not return until the sun reappeared.

The activities of any one insect are dependent not only on the weather and time of day but on internal factors as well; this is obvious on rather cold days when some males fly to water and others do not, the difference between the two groups being presumably the respective strengths of their reproductive drive. Sometimes this drive appears to be strong enough to send them to water but not to keep them there. The results shown in Fig. 2*d* may have resulted from such a conflict between reproductive drive and the effects of a strong south-westerly wind; these effects may

have been physical (temperature) or biological (lack of prey). On several other occasions when there was a strong wind *S. striolatum* were found at midday in a field half-way between their roosting area and the river.

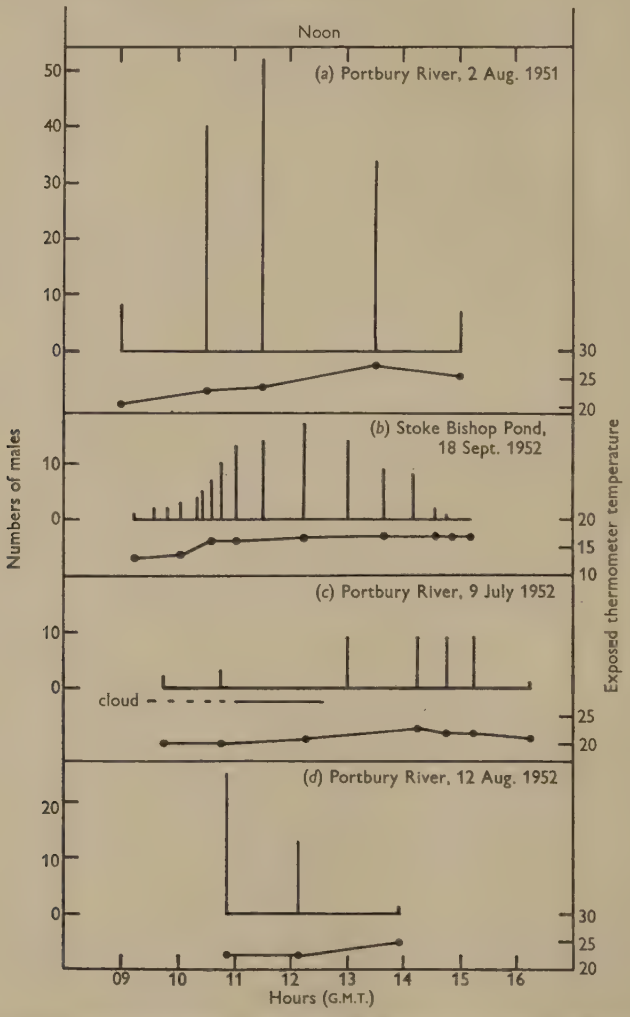

Fig. 2. The rise and fall in numbers of male dragonflies by water during the day. (*a*) and (*b*), on fine days; (*c*), on a cloudy day. ---, intermittent sun and cloud; —, continuous cloud with no sun. No dragonflies present at 1215 G.M.T.; population at 1300 G.M.T.—5 *Libellula quadrimaculata*, 3 *Orthetrum cancellatum* and 1 *Anax imperator*. (*d*), on a day of strong S.W. wind (force 5–6). Species present, *Sympetrum striolatum*.

The dependence of the daily rhythm of male dragonflies on regular fluctuations of solar energy, and its modification by variations in weather, is clear from the facts given in this section. But the exact temperature at which a male insect with high reproductive drive is prevented from going to water is not known. The lowest exposed

thermometer temperature at which adult dragonflies (*S. striolatum* and *Aeshna cyanea*) were seen flying both at and away from water was 13° C. The results of a preliminary investigation suggest that if their own temperature is above this they can fly at once on being disturbed, but if it is below, a period of wing vibration is necessary before flight can take place.

It has been shown above that the greatest densities of male dragonflies by water normally occur about noon on fine warm days. For the study of total population size and its fluctuation, it is necessary to know what proportion of the total male population of the area is by water at these times. It is impossible to count all the dragonflies when they are dispersed in their roosting area. Evidence provided by sample transects cannot be more than suggestive. Twenty-one such transects were made along the route indicated by the dotted line T_1 in Fig. 1. Altogether 58 adult male *Sympetrum*

Table 4. *Movements of* Sympetrum striolatum *between roosting and breeding areas, shown by counts made on a transect* (T_2 *on Fig. 1) at Portbury River, 16 September 1952*

Weather: much cloud 0900–1000 hr., decreasing thereafter. Wind N.E., force 3. (On previous 2 days approximately same direction and force 5.) Exposed thermometer temperature in sun in wind at noon 17° C. Exposed thermometer temperature in sun out of wind at noon 22·5° C.

Peak numbers for both sexes in roosting area (hedge), breeding area (water), and in the field between hedge and water are printed in heavy type.

Time (G.M.T.)	Air (shade) temperature (° C.)	Dragonflies on hedge (Y)		Dragonflies on field		Dragonflies by water (F, G and ditch E/F)	
		Males	Females	Males	Females	Males	Females
0905–0950	12·5	**1**	**1**	0	0	0	0
1015–1047	14·0	0	0	5	1	0	0
1107–1146	15·0	1	0	**12**	**6**	1	0
1153–1225	15·5	0	0	4	3	12	4
1227–1321	16·0	0	0	1	2	**25**	**5**
1417–1447	16·0	0	0	10	4	18	0
1525–1545	—	**3**	0	**10**	**6**	6	0
1600–1710	17·0	**7**	**2**	3	1	2	0

striolatum were counted, and only 14 of these were seen between 1100 and 1300 hr. G.M.T. Of 140 female and immature insects, 79 were seen between 1100 and 1300. No males of *Brachytron pratense*, *Libellula depressa* or *Orthetrum cancellatum* were seen between 1000 and 1400 hr., although females and immature insects were recorded. Three male *Libellula depressa* and six male *Orthetrum cancellatum* were seen earlier in the morning and later in the afternoon.

Occasionally, owing to a combination of warm sun and previous strong winds or other circumstances (see Penn 1950) dragonflies become concentrated in their roosting area, so that many more can be counted. Table 4 shows the results of counts made on eight transects, which included the F and G stretches of the Portbury River, and E/F ditch, the hedge (Y on Fig. 1) and the rough pasture between them (see T_2, Fig. 1) on 16 September 1952. They clearly indicate the daily rhythm of movement of *Sympetrum striolatum*: Hedge (roost) → Field → Water (breeding area) → Field → Hedge. They also suggest that the vast majority of males are present by water at noon.

(*b*) *Maximum densities*

The numbers of dragonflies in the sections (see Fig. 1) *A* (160 yd.), *B* (140 yd.), *C* (100 yd.), *D* (90 yd.), *E* (130 yd.), *F* (130 yd.) and *G* (100 yd.) were recorded on each count. The records for adult males were then expressed as number of dragonflies per 100 yd. of stream. The maximum figures for each section of stream for each year are given in Table 5. The number of dragonflies per unit area of water is a meaningless measurement, as far as the Libellulids are concerned, because their presence is

Table 5. *Highest densities of male dragonflies recorded from sections A–G, Portbury River, during 1949, 1951 and 1952*

Figures in brackets are from a count made at 1209 hr. 20 July 1951.

* At 1240 hr., 11 September 1951, 15 *Sympetrum striolatum* counted, i.e. 11·5 dragonflies per 100 yd.

BP = *Brachytron pratense*, *AI* = *Anax imperator*, *AC* = *Aeshna cyanea*, *Aj* = *A. juncea*, *LD* = *Libellula depressa* *LQ* = *L. quadrimaculata*, *OC* = *Orthetrum cancellatum*, *OCO* = *O. coerulescens*, *SS* = *Sympetrum striolatum*.

No records for 1950 were obtained after 29 June so records for that year are not included in the table. The greatest number of dragonflies per 100 yd. recorded in 1950 was 8·9 (section *D* on 11 and 29 June).

Section of river	Date	Time (G.M.T.)	Numbers of each species								Male dragonflies per 100 yd.
			BP	*AI*	*AC*	*Aj*	*LD*	*LQ*	*OC*	*OCO*	*SS*	
A	13 Oct. 1949	1210	—	—	1	1	—	—	—	—	11	8·1
A	28 July 1951	1220	—	1	—	—	—	6	14	—	3	14·9
A	25 May 1952	1210	4	—	—	—	1	6	—	—	—	6·9
B	8 July 1949	1430	—	3	—	—	2	2	5	—	—	8·6
B	20 July 1951	1029	—	2 (1)	—	—	—	4 (5)	7 (9)	—	12 (4)	17·9 (13·6)
B	25 May 1952	1440	7	—	—	—	1	8	—	—	—	11·5
C	12 July 1949	1440	—	2	—	—	2	2	4	1	2	13·0
C	20 July 1951	1029	—	(2)	—	—	—	6 (5)	3 (3)	—	4 (0)	13·0 (10)
C	25 May 1952	1210	7	—	—	—	—	5	—	—	—	12·0
D	5 Aug. 1949	1020	—	—	—	—	—	—	—	—	7	7·8
D	20 July 1951	1209	—	1	—	—	—	4	4	—	1	11·1
D	27 June 1952	1010	—	1	—	—	—	7	—	—	—	8·9
E	12 July 1949	1440	—	1	—	—	2	3	7	—	—	10·0
E	20 July 1951	1209	—	2	—	—	—	5	2	—	2	8·4
E	25 May 1952	1210	3	—	—	—	—	9	—	—	—	9·2
F	12 July 1949	1440	—	1	—	—	4	5	1	—	—	8·4
F	20 July 1951	1029	—	1 (0)	—	—	—	5 (7)	2 (1)	—	8 (1)	12·3 (6·9)*
F	12 June 1952	1207	—	—	—	—	—	7	3	—	—	7·7
G	13 Oct. 1949	1210	—	—	—	—	—	—	—	—	11	11·0
G	11 Sept. 1951	1239	—	—	1	—	—	—	—	—	10	11·0
G	3 Oct. 1952	1210	—	—	—	—	—	—	—	—	9	9·0

dependent on perching places and food supply, which are found mainly at the edges of the water. Both sides of a small stream or ditch are used by the individual dragonflies occurring by it. Therefore figures recorded from the margins of broad rivers and large ponds are not strictly comparable with those from narrow streams, because a part of one side only is used by each dragonfly which occurs by a lake. With the larger bodies of water the area of emergent vegetation is also an important factor. The measurement 'dragonflies per 100 yd.' was used in preference to 'yards per dragonfly' which would imply a regularity of spacing not usually found in nature.

In addition, numerous counts were made at other ditches in the Gordano valley, and by rivers, ditches, and peat cuttings elsewhere in Somerset and in East Sussex. A few of the records equalled, but only one exceeded, those obtained by the Portbury

River: at 1140 hr. G.M.T. on 25 May 1952, 16 *Libellula quadrimaculata* were counted on a 45 yd. stretch of the ditch marked *X* on Fig. 1, that is 35·5 dragonflies per 100 yd. Shortly after, this was reduced to 11 insects (9 *L. quadrimaculata*, 2 *Brachytron pratense*), that is 24·4 dragonflies per 100 yd. This density remained much the same till about 1520 hr.

Table 6. *Highest densities of male dragonflies recorded at Stoke Bishop and Abbots Leigh Ponds, 1951 and 1952*

AC = Aeshna cyanea, SS = Sympetrum striolatum.

Pond	Area (sq.yd.)	Edge* (yd.)	Date	Time (G.M.T.)	*AC*	*SS*	Males per 100 yd. of edge*
Stoke Bishop	*c.* 3900	*c.* 110	4 Oct. 1951	1235	1	21	20·0
Stoke Bishop	*c.* 3900	*c.* 110	5 Oct. 1952	1215	3	15	16·4
Abbots Leigh	*c.* 100	*c.* 40	13 Sept. 1952	1243	—	6	15·0

* Only edge found to be suitable for dragonflies is included in these figures.

Numerous counts were made at Stoke Bishop and Abbots Leigh ponds. The results obtained from them are to some extent comparable with those from the Portbury River and other ditches, and are given in Table 6. To summarize:

(1) The highest densities recorded from streams, rivers and ditches were 35·5 and 17·9 dragonflies per 100 yd.: the first at ditch *X*, the second at section *B* of the

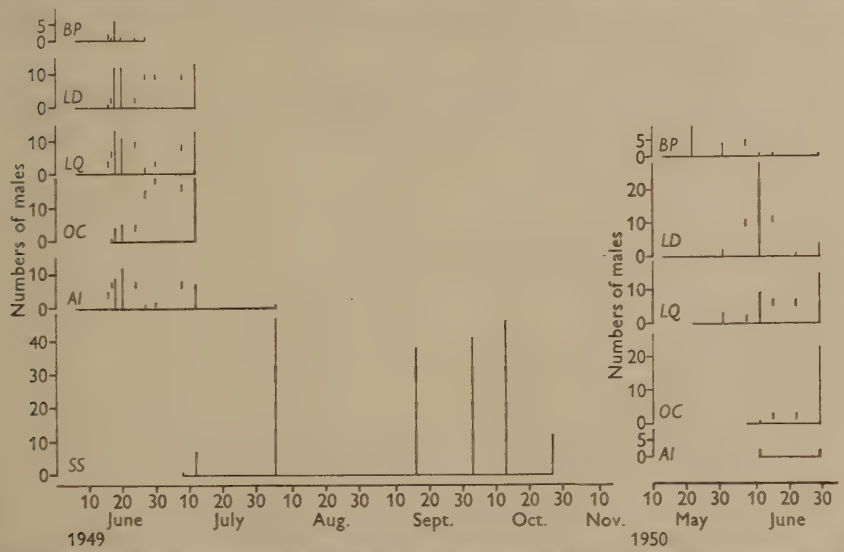

Fig. 3. The largest numbers of male dragonflies counted by water at Portbury River on the days indicated in 1949 and 1950. *BP*, *Brachytron pratense*; *OC*, *Orthetrum cancellatum*; *LD*, *Libellula depressa*; *AI*, *Anax imperator*; *LQ*, *L. quadrimaculata*; *SS*, *Sympetrum striolatum*. Base-lines indicate the lengths of observed seasons. Counts made about noon on fine days are represented by continuous lines, others by short dashes. In 1950 no counts were made from July to September; those in October are not comparable owing to flooding of the census area.

Portbury River. In neither case were these exceptionally high densities maintained; the noon density by the ditch *X* was 24·4 dragonflies per 100 yd., at section *B* it was 13·5 dragonflies per 100 yd.

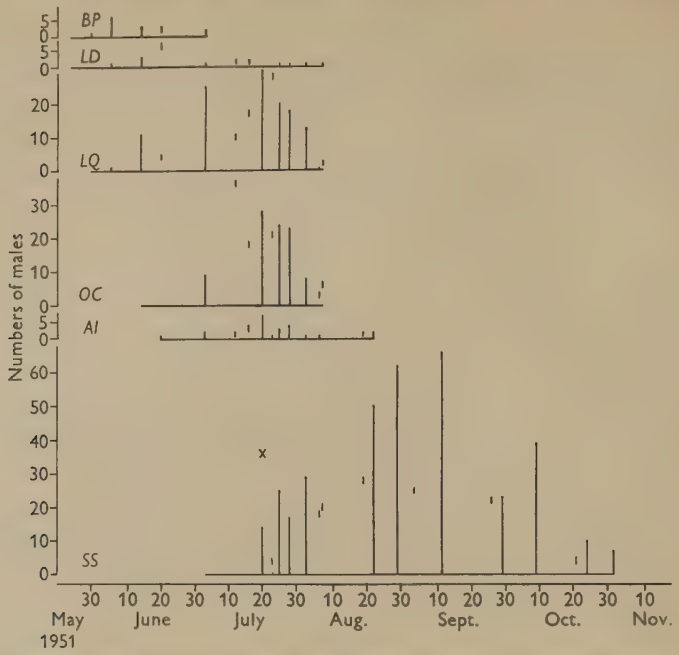

Fig. 4. The largest numbers of male dragonflies counted by water at Portbury River during 1951. *X*, number of *Sympetrum striolatum* counted at 1030 G.M.T.; other symbols as in Fig. 3.

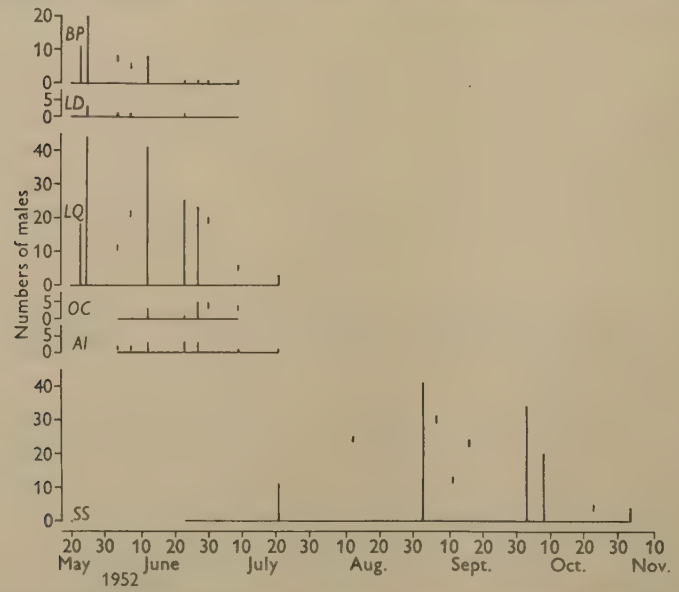

Fig. 5. The largest numbers of male dragonflies counted by water at Portbury River during 1952. Symbols as in Fig. 3.

(2) Apart from the records of unstable density, the highest densities recorded for each section of the river were (from *A* to *G*) 14·9, 13·6, 13·0, 11·1, 10·0, 11·5, 11·0.

(3) Although there was a remarkable numerical similarity between the records from all the sections (10–14·9 dragonflies per 100 yd.), the numbers of the different constituent species varied greatly, as did the times of year when maxima occurred.

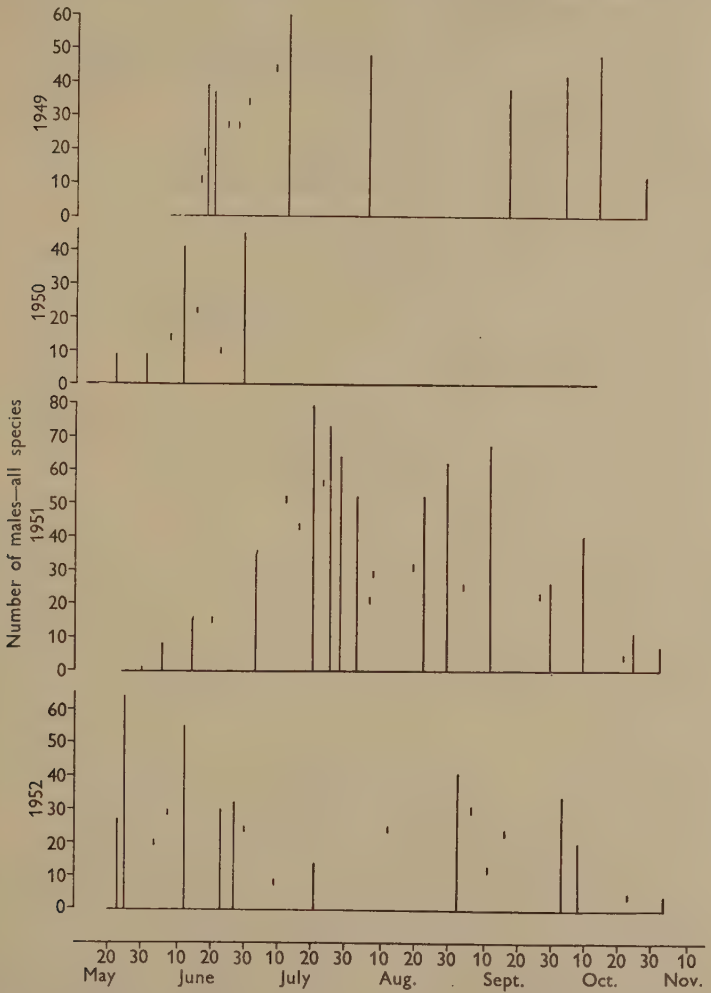

Fig. 6. The largest numbers of male dragonflies (totals of all species) counted by water at Portbury River on the days indicated from 1949 to 1952. Base-lines indicate lengths of observed seasons (all species). Other symbols as in Fig. 3.

(*c*) *Interspecific relations*

The data of the last section suggest that there is interaction between species. If this is so, the degree to which the seasons of the different species overlap would affect the densities of the species concerned. The seasonal changes in density of all the

species studied for four years are shown in Figs. 3–5. In Fig. 6 the numbers of all species are added together, and the total dragonfly populations for the four years compared. The overlaps of the species by Portbury River and for Stoke Bishop pond are summarized and compared in Fig. 7. The largest numbers recorded for each

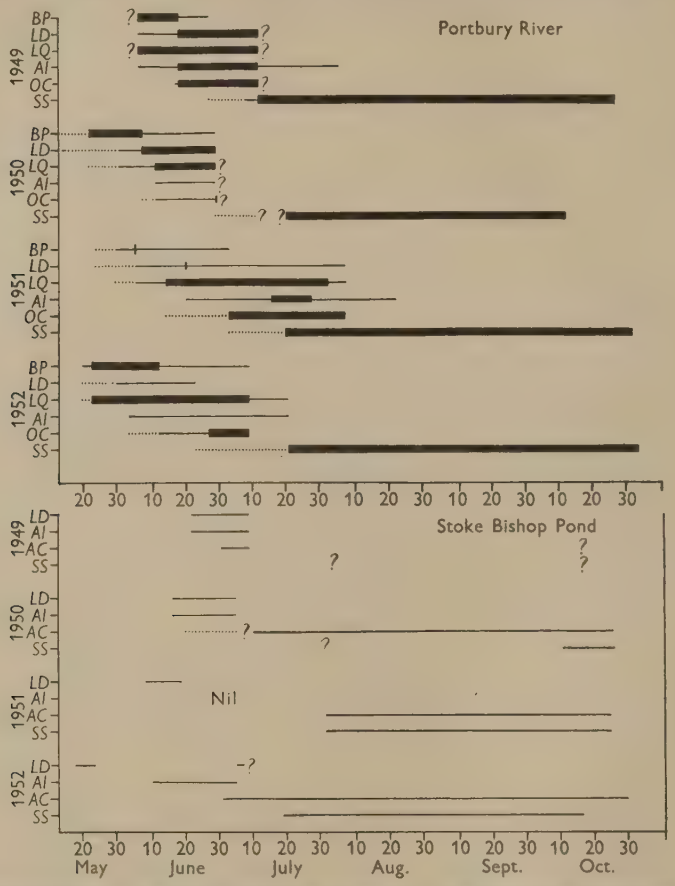

Fig. 7. The coincidence of seasons of the different species of dragonfly at Portbury River and Stoke Bishop Pond, 1949–52. *BP, Brachytron pratense*; *OC, Orthetrum cancellatum*; *LD, Libellula depressa*; *SS, Sympetrum striolatum*; *LQ, L. quadrimaculata*; *AC, Aeshna cyanea*; *AI, Anax imperator*. Occasions of first record of immature insect and first record of adult insect are joined by dots. Lengths of observed adult seasons are indicated by lines, narrow when < 4, broad when > 3 mature males were present (numbers indicated at Portbury River only). Where the first or last record was obviously later or sooner than the first or last occurrence it is marked ? (At Portbury River 1950 the only records for *Sympetrum striolatum* were the first immature and two mature insects in October. At Stoke Bishop pond in 1950 the only records for *Aeshna cyanea* were immature insects in June and July and mature ones in October.)

species each year are given in Table 7. Particular attention is drawn to the following facts:

(1) The season of any one species may overlap with that of any other species, except *S. striolatum* with *Brachytron pratense*.

(2) The peak periods of *Libellula depressa*, *L. quadrimaculata*, *Anax imperator* and

Orthetrum cancellatum are roughly coincident, although that of *O. cancellatum* invariably follows those of the other species.

(3) The first peak of *Sympetrum striolatum* may coincide with the end of the peak periods of the species mentioned above (as in 1951) or may not (as in 1952).

(4) The yearly sequence by Portbury River can be summarized as follows:

Stage 1: few days with low density and few species (*Brachytron pratense* dominant or sole species present).

Table 7. *Largest numbers of male dragonflies recorded on one count, 1949–52*

Portbury River

	Brachytron pratense	*Libellula depressa*	*Libellula quadrimaculata*	*Anax imperator*	*Orthetrum cancellatum*	*Sympetrum striolatum*	All species
1949	6	13	13	12	19	47	60
1950	9	28	15	2	23	*	45
1951	6	7	30	7	37	66	79†
1952	20	2	44	3	5	41	64

Stoke Bishop Pond

	Libellula depressa	*Anax imperator*	*Aeshna cyanea*	*Sympetrum striolatum*	All species
1949	2	2	‡	‡	‡
1950	3	2	‡	‡	‡
1951	1	0	5	21	22
1952	1	3	5	15	18

* Area flooded during peak period.
† At noon; 91 at 1029 hr. see p. 348 and p. 358.
‡ No records made during normal peak periods.

Stage 2: about 7 weeks with high density and four or five species (*B. pratense*, *Libellula depressa*, *L. quadrimaculata*, *Anax imperator* and *Orthetrum cancellatum*). Of these *Libellula quadrimaculata* was normally the dominant species, but all the other species were dominant on one or more occasions.

Stage 3: about 11 weeks with fluctuations in density of one species (*Sympetrum striolatum*), and irregular visits of very small numbers of Aeshnines (not shown in Figs. 3–5, or Fig. 7).

Stage 4: about 2 weeks with low and decreasing density of one species (*S. striolatum*) with occasional visits by Aeshnines.

(5) The relative abundance of the different species varied greatly from year to year.

(6) The difference between the highest and lowest maximum density recorded for each species over the four years was considerable.

Observations (unpublished) from other parts of Britain suggest that the variability of peak periods and coincidence of seasons shown at Portbury River is not exceptional. Very similar seasonal sequences are common elsewhere throughout the country. In those localities where *Orthetrum coerulescens* occurs, this species forms a connecting link between the early and late summer species, overlapping with both *Libellula quadrimaculata*, etc., and Sympetrines.

DISCUSSION

It has been shown above that whether 1, 2, 3, 4 or 5 species are present, the total density very rarely exceeds 13 males per 100 yd. of stream; and that normally the highest densities occur at noon, but the two abnormally high densities occurred in the

morning and were followed by more normal ones at noon. There can be no doubt that the daily maximal densities are controlled by a density dependent factor. But the food of dragonflies appears to be superabundant at noon on fine days. Also, the mature adult stages are very rarely preyed upon in Britain (Moore 1952*b*). In any case, neither the absence of food nor the presence of predators is likely to result in the short-term effects observed. These effects must therefore be the result of the behaviour of the insects themselves. The frequent and often violent clashes between male dragonflies of the same and different species are well known. Experiments designed to show the nature of these clashes suggested that they are reproductive rather than aggressive; the males attempt to mate with any other dragonfly they see flying. Nevertheless, observations showed that the clashes often lead to the avoidance of the place of encounter, and sometimes cause one insect to leave the breeding area (Moore 1952*a*). If the clash is between males of species which differ markedly in size, the smaller insect tends to fare worse. On 20 July 1951 the seasonal peaks of *Libellula quadrimaculata*, *Orthetrum cancellatum*, *Anax imperator* and *Sympetrum striolatum* coincided. Whereas the noon populations of all the larger species exceeded those of the morning the population of the small *S. striolatum* diminished from 36 to 14. This complete reversal of the normal daily rhythm was probably due to clashes resulting in the expulsion of the smaller insects from water.

What causes the density of about 13 male dragonflies per 100 yd. of stream (i.e. *c.* 8 yd. per dragonfly) to be critical is not known. This distance is not the same as the normal length of beat taken up by solitary insects, which is always more than 8 yd., and may extend for at least 170 yd. It is perhaps significant that the average length of stream occupied by one dragonfly when densities are highest is approximately the same as their range of movement perception; the writer recorded a range of 10–13 yd. in *S. striolatum*. Tillyard (1917) gives 20 yd. for the very large *Petalura gigantea* Leach.

Although the density of any population is the result of birth-rate, mortality and dispersal factors, the greatest emphasis is usually laid upon the controlling nature of the mortality ones. Because ultimately the total number of individuals of a species must be determined by mortality factors, it is often assumed that mortality factors control the density of parts of the total population. The present work shows that in adult dragonflies behaviour whose effect is density-dependent prevents further increase in adults long before mortality factors have any effect on density. Is the case of the dragonflies really exceptional? If overcrowding is biologically harmful and dispersal advantageous, natural selection might result in mechanisms which prevent the one and cause the other. The only pre-adaptation necessary would be sensory and nervous equipment sufficient to enable members of the species concerned to react differently under different density situations. The territorial behaviour of birds, etc., and the migrations of locusts, are probably examples of such mechanisms.

It is not of course suggested that predators and prey never control the densities of populations, but rather that density-controlling mechanisms are to be expected in the higher animals, however much their densities may at times be the result of mortality factors. For example, Varley (1947) showed that a population of the gall-fly, *Urophora jacobea* (Hering), near Cambridge, was controlled during 1935 and 1936 by the chalcid, *Eurytoma curta* Walker. But it was noted that 'the males are pugnacious,

and when two males meet they buffet one another with head and vibrating wings, or even grapple together, until one eventually retreats....It is almost as if each male maintains a territory as do the males of certain birds!' Without any first-hand knowledge of *Urophora*, this suggests to the present writer that in the absence of *Eurytoma* the density of the *Urophora* population would be controlled by the behaviour of the flies themselves.

ACKNOWLEDGEMENTS

I am indebted to Prof. J. E. Harris, in whose department this work was done, and who most kindly read the manuscript. Among other zoologists whom it is a pleasure to thank, for discussions and criticisms, I should like especially to mention my wife and my friend Mr Philip Corbet.

SUMMARY

1. Counts of the dragonflies by the Portbury River, Somerset and Stoke Bishop pond, Bristol, were made from 1949 to 1952 inclusive.

2. The daily movements between roosting areas and breeding areas, and the effects of weather on these movements, are described.

3. The majority of the males in populations of *Brachytron pratense*, *Libellula quadrimaculata*, *L. depressa*, *Anax imperator*, *Orthetrum cancellatum* and *Sympetrum striolatum* are present by water at about noon on fine days.

4. The total number of male dragonflies per 100 yd. of stream on seven adjacent stretches of the Portbury River were recorded. The number very rarely exceeded 13 dragonflies per 100 yd., whether 1, 2, 3, 4 or 5 species were present.

5. On two occasions much higher densities were observed in the morning, but by noon more normal densities were recorded.

6. It is suggested that the daily density of male dragonflies by water is regulated by their reproductive behaviour.

7. The degree of coincidence of the seasons of the species studied is shown to vary considerably from year to year. This probably affects the density of the species concerned.

8. The importance of density-regulating mechanisms in higher animals is briefly discussed.

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THE MECHANISM OF AGGREGATION IN BARNACLE POPULATIONS

A NOTE ON A RECENT CONTRIBUTION BY DR H. BARNES

By D. J. CRISP and E. W. KNIGHT-JONES

Marine Biological Station, University College of North Wales, Bangor

In a recent paper (Barnes 1953), an earlier suggestion that some barnacles incubate their larvae up to the cypris stage has been revived. This idea was put forward by Broch (1924) to explain large congregations of cyprids of *Balanus balanoides* observed swarming around adult barnacles in the intertidal zone (Runnström 1925). Although at no time has this explanation been substantiated by a direct observation of late-stage nauplii or cyprids in the mantle cavity of this or other species of *Balanus*, it has nevertheless been accepted by others as evidence of late liberations by incubating parents (Thorson 1946). Barnes has tentatively invoked the same idea to explain aggregations of *B. porcatus* da Costa (= *B. balanus* L.) which he has observed on *Pecten* shells, presumably making the further assumption that incubated cyprids do not migrate far by crawling, nor do they swim off before setting.

So far as is known with certainty prolonged incubation of larvae within the mantle cavity of cirripedes is confined to very few species, all but one being deep water or parasitic forms. Retention of developing larvae until they reach the cypris stage is known to occur in *Cryptophialus minutus* (Darwin 1854) and in certain species of *Scalpellum* (Barnard 1924, Nilsson-Cantell 1921) found in deep or moderately deep water, while direct development from the egg into a cypris larva has been described in two parasitic genera, the Rhizocephalan *Thompsonia* (Potts 1915) and an Ascothoracican *Dendrogaster astericola* (Knipowitsch 1891). The one species from the littoral zone, and the only representative of the Balanidae, in which incubation appears firmly established (Nilsson-Cantell 1921, Hiro 1939) is *Tetraclita divisa*, though other species of *Tetraclita* are known to possess free-swimming stages—*T. squamosa* (Yasugi & Ishida 1937), and *T. serrata* (Barnard 1924, Sandison 1953). We do not consider the evidence for prolonged incubation in *Ibla segmentata* (Broch 1922*a*, *b*), *Anelasma squalicola* (Kruger 1940, Frost 1928), *Mitella* sp., *Conchoderma auritum* (Broch 1927), and *Balanus balanoides* (Broch 1924) to be conclusive. In all the established instances of incubation there are relatively few ova, and these develop directly to the cypris stage, which is therefore little larger than the egg.

The remainder of the Cirripedia, of which a considerable literature exists, all produce many relatively small eggs which after hatching pass through six free-living nauplius stages with progressive increase in size. Incubation can be ruled out even as a remote possibility, for their microphagous feeding mechanism (Lochhead 1936) could scarcely be adapted to larval cannibalism in the brood pouch, nor is there in the adult any evidence of placentation. Moreover, in the course of studies of breeding, one of us (D. J. C.) has examined a total of 60,000 individuals belonging to the following

species: *Chthamalus stellatus*, *Balanus amphitrite*, *B. balanoides*, *B. crenatus*, *B. hameri*, *B. improvisus*, *B. porcatus* (= *B. balanus* L.), *B. perforatus*, *Verruca stroemia* and *Elminius modestus*. In no single instance has there been the slightest indication of retention of developing larvae. A few liberations have been observed in the laboratory; in these, fully developed embryos were discharged within their egg cases, and they immediately hatched in the surrounding sea water, liberating the first nauplius stage. For some unknown reason, embryos are occasionally retained within the mantle cavity for an abnormal term, but on such occasions they have been observed to decompose, although the parent often remains alive; they do not appear to undergo further development. Conversely, embryos are sometimes liberated prematurely, for they are occasionally found in the plankton not having hatched. These phenomena are clearly not associated with normal development.

We therefore consider that in all the commonly occurring barnacles of the order Thoracica, the cypris stage is attained only after a prolonged planktonic life. Aggregation of settled individuals must therefore be explained as a consequence of the searching behaviour of formerly widely dispersed cypris larvae before attachment. A description of the behaviour which leads to aggregation has now been given (Knight-Jones & Crisp 1953, Knight-Jones 1953).

Barnes has also suggested that a distinct period elapses before the cypris stage undergoes a physiological change leading to crawling and initial attachment. This period is either short or non-existent in at least one species, since we have found that *Balanus crenatus* will settle gregariously within twenty-four hours of the final moult from the last nauplius stage. Moreover, given suitable *in vitro* conditions, cyprids of *B. balanoides* and *Elminius modestus* taken from the sea will set mostly within a few hours, and all within a day or two, although, as Barnes correctly surmises, setting can be delayed if conditions are unsuitable.

An important ecological feature relating to the limitation of certain species (e.g. *B. balanoides*) to the intertidal zone, is perhaps not generally recognized. The cyprids of these species, like those of sublittoral barnacles, settle and begin to metamorphose entirely below water-level, and can effect the whole process without exposure to air (Pyefinch 1945) and also in total darkness. Although the appearance of countless cyprids between the tidemarks gives the impression that they have been stranded by the receding tide and so induced to settle within the littoral zone, this is not so. Indeed cyprids of *B. balanoides*, if exposed to air whilst crawling, soon release their hold and withdraw their antennules, and so would be washed off by subsequent waves. The restriction of the species to the shore must therefore be due to other causes, of which the most important would appear to be surface swimming and gregarious setting. This behaviour probably accounts for the swarming of cyprids at the water's edge, especially as the tide recedes. At the height of the setting season many hundreds of cyprids may be collected in a few minutes by shaking handfuls of *Fucus* into large wide-mouthed jars (breffits) filled with sea water, when cyprids crawling on the *Fucus* are disturbed and swim off into the jars. Observing the cyprids in such dense concentrations, it would be easy to draw the false conclusion that they had just been liberated by the neighbouring barnacles.

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REVIEWS

BRITISH ETHOLOGY

The British Journal of Animal Behaviour. Vol. 1, nos. 1 and 2 (January and April 1953). London: Baillière, Tindall and Cox for the Association for the Study of Animal Behaviour. Published quarterly; annual subscription 27*s*. 6*d*. (U.S.A. and Canada $5.00).

As their science progresses beyond the descriptive phase into that of experiment and the search for reasons and mechanisms, animal ecologists will inevitably acquire a closer interest in behaviour. The appearance of a new journal devoted to this subject is therefore an event of some moment. The Association for the Study of Animal Behaviour was founded in 1936 to bring together those zoologists and others whose interests lay in this direction, and it is satisfactory to know that the association has progressed sufficiently to replace the *Bulletin of Animal Behaviour*, which appeared irregularly, by this new *Journal*, which will be published quarterly, as its official organ. The *Journal* is edited by Alastair N. Worden and B. A. Cross, who are assisted by an impressive board including most of the important names in the subject.

An editorial by the President of the Association for the Study of Animal Behaviour, Dr W. H. Thorpe, F.R.S., opens the first issue. This article makes it clear that the new *Journal* is not intended to be quite an ordinary scientific journal, and is in particular not to overlap with the field of *Behaviour* which was founded with the Association's co-operation. The intention is to publish a proportion of articles of the review or summary type, and especially to foster co-operation between ethologists and those whose main concern is with the breeding and observation of domesticated animals, and to bring to the notice of the latter group of people the opportunities their work affords for research on the behaviour of their charges. These objects are presumably the justification for the somewhat 'magaziney' effect produced by the double column format with lavish use of Clarendon type in cross headings, an effect enhanced by the small numbers (no. 1, 40 pp.; no. 2, 50 pp.) clipped through the centre with wire staples.

No. 1 contains seven papers of which two (one of them a short note of a single page and a table) describe original observations and experiments—on bees and wild rats respectively. Of the five papers in no. 2, three are of this type and deal with grouse, bees and bullocks. There follows an account of a symposium on 'Behavioural Aspects of Shore Ecology', with précis of the papers given, which will be read with interest by marine and other ecologists, but are nevertheless not solid contributions to knowledge in the rigorous sense of that phrase. On the merits of the articles it would be presumptuous for us to comment, but most of the work described and of the subjects discussed are likely to interest ecologists, and we feel sure that the editors are fully aware of the danger, which obviously besets them, of 'talking down' to their public, apparently only partly composed of scientists. We shall watch the *Journal's* progress with interest and good-will and we hope to see it established on a strongly built bridge securely founded on the two stools 'scientific journal' and 'popular magazine'. H. C. GILSON

SOIL MITES

K. Strenzke (1952). Untersuchungen über die Tiergemeinschaften des Bodens: die Oribatiden und ihre Synusien in den Böden Norddeutschlands. *Zoologica*, **37** (104), 1–174: with 1 plate and 10 text-figures.

Until recently the study of the ecology of invertebrate communities in the soil has been almost impossible, because the taxonomy and general biology of each group was the province of a few overworked specialists. This state of affairs is now changing, thanks largely to the efforts of taxonomically minded ecologists and ecologically minded taxonomists who are making it possible for the ecologist—still not without considerable labour—to carry out combined studies covering at least the most important groups himself. The assistance of the taxonomist is still of course essential, but the preliminary census work can now be carried out on a group such as the oribatid mites by the ecologist who has but a year or two's experience of these animals.

Following his important studies on the Dipteran larvae and the Collembola of moist soil localities Dr Strenzke has now published a parallel and more detailed study of the oribatids from the same area. His credentials as an acarologist are indisputable; he has described many species and illuminated many difficult taxonomic problems; but the present work is much more than a check-list or a mere tabulation of collections. Half the work is a detailed survey of the north German and Holarctic distribution of over 240 species and subspecies, with an analysis of the main habitat factors of their characteristic localities. This list covers just over half the species so far recorded for Britain; 102 and 125 species respectively are peculiar to Strenzke's list and to Dr Turk's new check-list (1953, *Ann. Mag. Nat. Hist.* **6**), while 122 are shared by the two faunas. This part is made the more useful to British acarologists because Dr G. O. Evans contributed the notes on the British distribution.

The description of the ecological requirements of the species follows a procedure which, while not popular in this country, is a great advance on anything previously available. The author's own collections were correlated with assessments of soil water content, humus content, pH and litter cover. Each sample was then scored on a scale of 'low' 'moderate' or 'high' for these four factors. For nearly half the species a detailed analysis of the number of samples containing that species and falling in each category is then given, and in this way quite clear ecological ranges are brought out. Had the collections been less restricted to areas of damp, humus-rich soils the results would have been more spectacular. This part of the work is supplemented by a series of chapters on each of the four main environmental factors mentioned, and also of the soil salt content.

The author contends that a knowledge of the oribatid fauna can form the basis of a useful classification of soil-types and supports this in a chapter on the 'ecological valency' of these mites. For each factor in turn Strenzke gives a table in which the species are grouped in order of their positive or negative association and also the extent to which their distribution is confined to a narrow part of the range or is more universal. These conditions are described by such expressions as 'poly-steno-hygr' (meaning confined to areas of high water content). To a very large extent the tables agree with the subjective impressions of an English soil ecologist, while the conspicuous exceptions (such as that *Scheloribates latipes* is predominantly a mite of areas without litter cover and that *Hypocthoniella pallidula* is restricted to acid conditions) point at once to interesting ecological differences in the two countries. The 'ecological valency' of certain selected species is also described by means of histograms which show very clearly the contrast between the 'stenöke' forms such as *Chamobates pusillus* and *Phauloppia lucorum* and the 'euryöke' species of which *Scheloribates laevigatus* and *Tectocepheus velatus* are examples. It is shown that, over the range of habitats studied, most species of oribatids are found in conditions of moderate moisture and litter cover and high humus content and acidity.

Chapters on phenology, vertical distribution and life-forms follow and deal, in addition to better known topics, with the number of generations per annum, variations in numbers between successive years as well as from season to season, the differences in vertical migration of different species and the characteristic differences in life-form of the surface-dwelling as compared with the true soil forms. These are all subjects which have been virtually ignored in this group.

The remainder of the work is concerned with the six main oribatid 'communities' which are associated with corresponding distinct types of habitat. Six clear photographs are particularly useful to the foreigner. Some data are also given for other groups of mites, including Mesostigmata, Trombidiformes and Tarsonemini and of insects such as Collembola and Chironomidae. By means of tables those species and samples are grouped together which have the greatest faunal similarities, and in this way a whole classification of 'vereine', 'synusie' and 'variante' is created, according to the principles evolved for animals by Gisin (1943, *Rev. Suisse Zool.* **50**, 131–224) and by Strenzke himself (1949, *Z. PflErnähr. Düng. Bodenk.* **45**, 245–62). The fact that a number of different communities may co-exist at different depths is demonstrated and considered to be important. Vicariant species are used as far as possible to describe the different communities which are those of:

Salt meadows and damp sea shores (*Oribatella arctica littoralis*).
Wet meadows and alder woods (*Gustavia fusifer-Liebstadia similis*).
Floating and saturated acid peat bogs (*Limnozetes ciliatus*).
Very acid bog and wet forest soils (*Nothrus silvestris*).
Dry moss and lichen-covered surfaces (*Zygoribatula exilis*).
Algae and submerged moss of neutral eutrophic waters (*Hydrozetes lemnae*).

The interrelations and affinities of these communities and their minor variants are considered in detail, and it is shown that they are mainly differentiated by humidity and pH. The oribatid fauna of cultivated fields bears the closest resemblance to that of the shore meadows of eutrophic lakes, and of damp woods.

The most marked feature of studies of this kind to the British ecologist is the absence of quantitative data. The question of efficiency of extraction methods is not even discussed in this paper, and there is a welcome simplification of technique and concentration on the understanding of the environment where the animals actually live. Only orders of abundance of the different species in rather small numbers of samples are used. In this way it has been possible to outline the limits of tolerance of the species to a few rather arbitrarily selected physical factors—an important beginning indeed. It is difficult for the British ecologist, however, to understand how such methods can be used to determine the structures of the communities and the detailed distribution of the fauna. Thus for each of the physical factors about half the species fall into a single most abundant category of moderate water content, high organic matter content, low pH and moderate litter cover. A high proportion of animals must be common to these four classes. However, it is certain that all these species would not in fact be found together in a single locality which combines these four attributes. It is surely here that one must begin the study of biotic communities *per se* as distinct from that of the physical limits of their range.

Dr Strenzke has thus provided an invaluable foundation for the study of a group, the number of species of which, as he remarks, frequently outnumber those of all other arthropods; he has distinguished the main ecological communities within a wide range of soil types and collected together the published data on holarctic distribution. He has thus made accessible to the ecologist a field which was virtually unapproachable before. A. MACFADYEN

AMERICAN METHODS IN FRESH-WATER FISHERY BIOLOGY

Karl F. Lagler (1952). *Freshwater Fishery Biology.* Pp. x+360; 184 text-figures including many photographs. Dubuque, Iowa: Wm. C. Brown. Price $5.75.

In North America the State managements of fresh-water sport fisheries have become large-scale undertakings, and now employ considerable numbers of biologists. *Freshwater Fishery Biology* is intended primarily to be a text-book for the training of these biologists, and is based on courses given by the author at the University of Michigan.

The book describes, often with lucidity and just the right amount of detail, most of the methods employed in American fishery biology. Among the many aspects covered are the collection of fish samples, taxonomy, stomach analysis, scale reading, creel censuses, artificial fish hatching, fish pathology, some simple methods in physical and chemical limnology, making and stocking fish ponds, and fishery legislation. Considerable emphasis is laid on the conventional methods of collecting and recording data, even to the provision of sample forms to be filled in for each type of information recorded. There is much useful information, many reference tables, and generous lists of references to the literature; so that anyone of average intelligence should be able, with this book as his guide, to carry out a lake or stream survey or conduct a simple conventional investigation into the ecology of a fish species.

Bearing in mind the background, aims, and title of the book, and the several quite excellent features mentioned above, attention must, however, be drawn to certain grave failings. Many of the methods and techniques described are not the best now available, and several quite widely known and useful hints and tips have been omitted; perhaps the author has been a little too parochial in his sources. The previous knowledge expected of the reader is a little strange. For example he apparently should know all the conventions and methods of fish taxonomy, but not that fertilization is the union of egg and sperm nuclei, and should know a fair amount of statistics, but not that the area of a circle is given by πr^2. The chapter on populations is quite inadequate, as there is no mention of mortality-rates and the concepts of biomass and production. Throughout the book there is hardly any mention of the statistical problems of sampling; even if it is assumed that the reader has some knowledge of these, it is still clear that the designer of many of the methods described was ignorant of them.

One major general criticism is that the methods and details are too stereotyped and conventional, and presented too much as ends in themselves. The reader might have been expected to use his intelligence and imagination to a much greater extent, and students trained with the

aid of this book will tend to become technologists rather than scientists. Considerable space could have been saved by omitting, shortening, and avoiding duplication in the lists and facsimile forms, many of which must apply to only very limited situations.

The greatest failing of this book is, however, its concentration on the collection of material and its comparative silence on what is supposed to be done with all the raw data once collected. Do the State conservation departments employ mystical genii who can digest in a twinkling an omnivorous diet of areas, depths, oxygen contents, fish fauna lists, growth-rates, creel census returns, etc., and then come out with a detailed, scientifically based management policy for a few hundred newly surveyed lakes each year? Surely those responsible for feeding these beings should have some knowledge of their digestive processes? Most ecologists soon find that information collected because 'it might be useful' very rarely proves to be so, and that in collecting raw data the exact aims of the investigation, and the processes by which the data will be analysed must be borne clearly in mind. Thus, even if Dr Lagler intended to confine his book (in spite of its title) to the methods of collecting and preparing raw data, he should have given us some clearer picture of the principles involved in fishery management, and exactly how the biological information collected with such labour can be put to use.

In spite of these failings this book will doubtless prove to be useful, and it does at least partially fill a void which has long been prominent in fishery literature. Ecologists will find some useful methods; fishery biologists will find it informative and a valuable reference, though they will not wish to follow it to the letter and should be wary of adopting its methods for their own, or convention's sake, rather than in relation to the more fundamental aims of their work.

E. D. LE CREN

J. R. Harris (1952). *An Angler's Entomology.* Pp. xv+268; 42 plates; 10 text-figures; 17 maps. New Naturalist Series. London: Collins. Price 25*s*.

Probably because I am a biologist and not an angler, I find this a strange book, but I am sure that anglers will rightly regard it as the best of its kind yet written. It is full of interesting facts and observations on aquatic insects, chiefly Ephemeroptera, and brings together in very readable form much scientific work. Some of the subject-matter is of the calibre one would expect to find in a general scientific work such as *Die Tierwelt Deutschlands*, but at intervals the author slips, rather incongruously, into the jargon, and, dare one say, superstition of anglers.

Mr Harris has set out to write a book which will enable anglers to identify the more important insects they are likely to meet, and which will stimulate an interest in the flies themselves. With the keys, detailed descriptions and excellent colour photographs, identification of the mayflies, and to some extent of the stoneflies, should prove easy.

The chapters in Part One of the book will undoubtedly fascinate anyone who is interested in the general natural history of the mayflies. Mr Harris describes the structure of the various stages, life-cycle, adaptations of nymphs, emergence, mating, oviposition, general ecology, distribution and enemies. This part is pleasingly written and shows itself to be based on intimate knowledge and much careful observation. Some of the aspects discussed, such as behaviour at and shortly after emergence, the various types of swarming flight of the adults, and details of oviposition, have never before been so well described. It is this part of the book that will most appeal to the biologist. Of very great interest also are the maps of Britain giving details of the known distribution of several species. Obviously these maps are incomplete, but they are a valuable first step in what one hopes may become a general study of the distribution in Britain of the aquatic insects.

Part Two deals rather briefly with the Trichoptera, Plecoptera and Diptera. The information given is more scrappy than that in Part One, and has not the same air of personal acquaintance which makes Part One such good reading. One feels that more could have been made of the Trichoptera and their varied larval habits. Nevertheless, Mr Harris undoubtedly brings the existence and interest of these orders to the notice of the angler reader.

Part Three, entitled 'Flies and Fish', is, to me, the least satisfactory section of the book. It consists of five chapters entitled: 'Period flies and modern names', 'Tastes of fish', 'A note on surface tension' and 'Notes on fly dressings'. The first is a worthy and not unsuccessful attempt to bring some sort of order to the chaos of anglers' names for flies. The second deals very briefly, and rather inadequately, with what is known of the feeding habits of trout. Its chief purpose seems to be to show that trout discriminate in their choice of food, and that they tend to choose

only one type of organism at a time. What it does not mention is that, although the fish are often found to have been feeding on one organism alone, this does not necessarily indicate a choice but may merely reflect the position of the fish at the time of feeding and the behaviour of the invertebrate involved. It also fails to point out that even in rod-caught fish the majority of the animals found in the stomach are usually not flies in the anglers' sense at all. Frankly I regard this chapter as a piece of special pleading. The chapter on 'Flies and fish' describes the various species of fly in chronological order of their appearance on the water, and lists the lures which the author considers will catch fish when each is on the wing. This is an aspect of fly-fishing in which I personally can never believe. Artificial flies often only remotely resemble the real thing, and anglers have told me that the fly which kills is often not even supposed to resemble any natural fly which is present at the time. Also, if one may quote him against himself, Mr Harris, in discussing the artificial alder fly, states that it is often successful even when *Sialis* is not on the wing, possibly because it resembles a dark sedge fly, a large heavy fly of the blue-bottle type or a beetle. If a single artificial fly can resemble all these varied insects can one really believe that fishes can appreciate the subtle differences between the various species of Baëtidae? Surely it is more honest to admit that the fish take artificial flies because they mistake them for insects, that sometimes one pattern is effective while others are not, and that the study of natural flies is not very helpful in choosing which artificial one to use, but that it is fascinating for its own sake. After all, most anglers fish more for the pleasure of being by the river than for the filling of their kreels, and a knowledge of and interest in the flies can only enhance that pleasure, especially when the fish are being difficult! Is that not just what Mr Harris has found, and why he has written such an attractive book?

H. B. N. HYNES

BRITISH MAMMALS

L. Harrison Matthews (1952). *British Mammals.* Pp. xii + 410; 64 plates; 92 text-figures. New Naturalist Series. London: Collins. Price 25*s.*

It is over forty years since the first parts of Barrett-Hamilton's uncompleted *History of British Mammals* were published. Since then no other major work on this subject has appeared, although in the meantime great advances have been made in many branches of mammalology, notably in the study of populations, reproductive physiology and genetics. If the value of a new book on an old subject is to be judged by the amount of new information it contains, Dr Harrison Matthews' *British Mammals* must be rated as of the highest importance. He has set out to write a comprehensive account of the general biology of our native mammals taking into account all the important work on them up to 1950. The magnitude of this task may be seen by a glance at the bibliography of 234 references, of which the great majority has been published during the past twenty years. Among the topics discussed for the first time in a general work of this kind are the echo-location system of bats, the cyclic fluctuations in populations of small rodents, the problems of the respiration of seals and whales, the delayed implantation of Mustelidae and many more on which almost all our information has been gained in recent years.

The design of the book is simple and logical. Following an introductory chapter on the general structure and organization of mammals, the various members of the British fauna are dealt with in their natural groups. The Insectivores, the terrestrial Carnivores, the seals and the deer receive a chapter each, and two chapters each are devoted to the bats, the rabbits and rodents and the whales. The account of each group is self-contained. Naturally those animals which are the author's special interests receive the most attention, and it is largely his own researches that give these sections their special importance. The chapter on the biology of whales for instance is probably the best account of its length that has ever been written, and the descriptions of the life of bats and seals are equally outstanding. Throughout an excellent balance has been struck between the presentation of established facts and the discussion of outstanding problems. The style is clear and forthright. The author is never afraid to state his own point of view without forcing it unduly, and the reader is continually taken up to the very frontier of our knowledge.

Although no doubt prevented by considerations of space, it seems a pity that the semi-feral mammals such as the Soay sheep and our 'wild' white cattle do not receive fuller treatment. As the author himself says they form a fascinating study of their own and a chapter on them would have been a welcome enrichment to the book.

The final chapter on the origin of our mammal fauna is disappointing, and gives the impression that the author has been content to rely mainly on the views of other workers. To do justice to this complex problem requires a more searching discussion of the mechanism and speed of evolutionary change under different conditions, as well as the more familiar interpretation in terms of waves of immigration from the Continent during the periods of glacial recession.

The numerous text-figures, nearly all of them original sketches by the author, deserve a special word of praise. There are also forty-eight plates in black and white, and sixteen in colour. The former are excellently chosen, but some of the colour plates are not so satisfactory. In particular, those of the bank vole and the red squirrel, which are hand-coloured from black and white photographs, would probably have been better in their original form. In the bibliography, number eighty-eight should refer to the American *J. Exp. Zool.* and not the British *J. Exp. Biol.*

These are, however, minor points which do not affect the editors' claim that this is the most important book on the British mammals that has ever been published, a statement with which the reviewer is in full agreement. D. M. STEVEN

D. R. Rosevear (1953). *Checklist and Atlas of Nigerian Mammals with a Foreword on Vegetation.* Pp. 131; 33 plates; 104 maps; 2 folding coloured vegetation maps. Lagos: The Government Printer, Nigeria. Price 10*s.*

This book is much more interesting ecologically than most check-lists. It has been compiled by the Inspector-General of Forests, Nigeria, who writes a useful foreword about the vegetation zones of the country. He points out that most if not all of the forests, even when well developed, is secondary growth after human interference; but that the habitats and the fauna are very varied. The photographs of vegetation though not always technically first-rate give a clear notion of the habitats. 239 species of mammals are listed, and a synopsis for each is given of its range, habitat, type locality and known races. A map for each species shows the authenticated spots of occurrence, within a wider area of probable range based mainly on the habitat type. The coloured vegetation map of Nigeria on a scale of about 1 in. to 47 miles, can be compared with a more generalized smaller-scale map of West and Central Africa. This book seems to be usefully planned as a basis for more intensive studies. C. S. ELTON

AUSTRALIAN SEASHORES

W. J. Dakin (1953). *Australian Seashores.* Pp. xii + 372; 99 plates (some in colour); 23 text-figures. London: Angus and Robertson. Price 45*s.*

There appeared in 1939 a remarkable book* which attempted, for the first time, to give an account useful to both amateurs and professionals, of the seashore life of a very long coastline, the Pacific coast of North America. This was supplemented in 1941 by a similar work,† extending the survey farther south, and but for the untimely death of the author common to both, E. F. Ricketts, a third volume continuing the work northward would also have been forthcoming. The book here reviewed, by W. J. Dakin, is a successor in the same vein to those of Ricketts, and in this case also the chief author is unhappily dead. His death before the appearance of the book has affected it less than might have been feared, however, as he had two very able assistants in his work, Isobel Bennett and Elizabeth Pope, who saw the volume through the press.

It is a feature of all the books mentioned that they are heavily illustrated, and Dakin's volume is no exception. It has 99 plates, most of them reproduced from monochrome photographs, which are of excellent quality and give a most vivid and adequate idea of the plants and animals of the shore, and of their arrangement in groups and zones, as well as of the scenery of the coastline. Among the plates are a few coloured ones, mostly from photographs, and one of these is particularly interesting, as it shows an astonishing range of colour-variation in the shore starfish *Patiriella calcar*, covering most colours of the rainbow, including blue. This forms a

* Ricketts, E. F. & Calvin, J. (1939). *Between Pacific Tides.* Stanford University Press. Second and third editions in 1948 and 1952.

† Steinbeck, J. & Ricketts, E. F. (1941). *Sea of Cortez.* Viking Press.

parallel to the similar range found in South African individuals of the Indo-Pacific *Asterina exigua*. These illustrations constitute an invaluable source of reference to anyone needing to make preliminary identifications of common Australian shore animals, and also a basis of comparison between these creatures and their counterparts elsewhere in the world.

The text is arranged according to the following plan. The first eight chapters are introductory. The first gives a preliminary account of the Australian coast, of the arrangement of organisms along it, and of its subdivision into geographical provinces. (The book, while referring to a certain extent to Australia as a whole, deals primarily with New South Wales.) The second is a very general chapter on the sea itself. The third deals with the tides, the fourth with ocean waves and their effect on the coast, the fifth with the sculpture of coastlines, and the sixth with the plankton. The seventh and eighth discuss luminescence and coloration. These early chapters take us to page 84, leaving the main part of the book for the more detailed consideration of the shore and its population. This begins with an account of the zonation of plant and animal life on the rocky shores of New South Wales, and continues with a description of some of the seaweed growths of the rocky ocean coast. The next eight chapters deal with the shore animals, considering them group by group, so that the sponges are described in one chapter, the coelenterates in another, and so on. The volume ends with 'afterthoughts' and a note on flotsam and jetsam.

The book has a great deal to commend it. Not only does it serve as an introduction to marine biology, with special reference to Australia, but it brings together a mass of detailed information about common Australian plants and animals which has never before been available in a single book, and to which the authors themselves have contributed a great deal of new material. In other words, it makes the study of shore ecology much more practicable for students of Australia, than it ever has been before. It should be added that there has, in recent years, been a marked advance in our knowledge of the shore ecology of Australia, Tasmania and New Zealand, to which a number of authors, including the writers of this book, have contributed.

From an ecological point of view there are several matters of interest covered by the book. It has been a curious feature of the geographical study of the Australian coast, that a section of its fauna and flora has largely been overlooked until recently. In his *Zoogeography of the Sea* (1935, 1952) Ekman treats the whole of Australia south of its tropical parts as a warm-temperate area, basing his view on the work of other authors who have taken the same line. In 1947 (in a paper dealing with the South African coast in its world-relations) I pointed out that the southern part of New Zealand and possibly part of Southern Australia would probably prove to be cold-temperate when more was known of them, and this expectation has been fully realized. In the book under review it is clearly shown that the Victorian, Tasmanian and Southern New Zealand coasts must be classified as cold-temperate areas, although each of them has its own distinctive variations. From the point of view of intertidal zonation, also, the book makes a very definite contribution, providing a clear account of the arrangement of the zones in New South Wales, and of their variations. A valuable note has been added (as an appendix to Chapter IX) by Bennett and Pope, summarizing recent work, carried out since the chapter was written, on the changes in zonation which are observable as one follows the Australian coast round from New South Wales through Victoria and South Australia to Western Australia.

Altogether, the book represents a most valuable contribution to knowledge, upon which all three authors may be sincerely congratulated.

T. A. STEPHENSON

BOOKS RECEIVED

Zoogeography of the Sea. By Sven Ekman. Translated from the Swedish by Elizabeth Palmer. London: Sidgwick and Jackson. 1953. Price 42*s.*

Methods and Principles of Systematic Zoology. By Ernst Mayr, E. Gordon Linsley & Robert L. Usinger. New York, Toronto and London: McGraw Hill. 1953. Price 51*s.*

Social Behaviour in Animals with special reference to Vertebrates. By N. Tinbergen. London: Methuen. 1953. Price 12*s.* 6*d.*

The Social Insects. By O. W. Richards. London: Macdonald. 1953. Price 15*s.*

Climate and the British Scene. By Gordon Manley. London: Collins. 1953. (New Naturalist Series.) Price 25*s.*

Rats and Mice on the Farm. Ministry of Agriculture and Fisheries, Bulletin No. 30. London: H.M.S.O. 1953. Price 2*s.*

ABSTRACTS

This issue of abstracts brings the series up to date with most of the journals which the existing rather small panel of abstractors can cover. There remain outstanding a number of publications which cannot be dealt with unless more offers of help are volunteered.

The abstracts are edited by Prof. L. A. Harvey with the assistance in selection and abstracting of J. D. Brayshaw, D. H. Chitty, G. I. Crawford, M. J. Delany, A. E. Ellis, Miss U. Grigg, N. A. Holme, A. Macfadyen, C. Matheson, Miss E. Nelmes, G. G. Vickers, and M. Williamson. References are checked by B. M. Hobby. Mr R. S. R. Fitter, with the help of the societies themselves, aims to cover all the proceedings, transactions and journals of local natural history societies and field clubs. Secretaries of such organizations can greatly aid this work by sending, regularly, copies of their publications to **R. S. R. Fitter, Esq., Drifts, Chinnor Hill, Oxford.** Readers and authors can materially assist by pointing out errors and omissions, and by sending reprints or offers of help in making abstracts to **Prof. L. A. Harvey, University College, Exeter.**

It is hoped to publish in the next issue a complete list of publications which are regularly abstracted, coupled with a list of those which it is considered desirable to cover as sufficient help becomes available.

Separate copies of the abstracts printed on one side of the paper can be obtained from **The Cambridge University Press, 200 Euston Road, London, N.W. 1,** or through any bookseller; price 5*s.* 6*d.* per annum, post free (issued in May and November). Back numbers of the 'Notices of publications...' from Vol. 3 (1934) to Vol. 20 (1951) may also be had at 2*s.* for each annual set of two parts.

CONTENTS

NOTE. In order to avoid unnecessary overlap with journals which the ecologist would be likely to consult in any case, papers in the *Journal of Animal Ecology* are not noticed, nor are:

(*a*) papers in *Bird Notes* and *British Birds* which would fall in '4. FOOD AND FOOD HABITS',

(*b*) papers in the above two journals and in *The Entomologist*, *The Entomologist's Record* and *The Entomologist's Monthly Magazine* which would be classified in '5. MIGRATION, DISPERSAL AND INTRODUCTIONS'.

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1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(*a*) MARINE AND BRACKISH

Bainbridge, R. (1952). Underwater observations on the swimming of marine zooplankton. *J. Mar. Biol. Ass. U.K.* **31**, 107–12.

By the use of compressed-air breathing apparatus underwater observations have been made on the swimming-movements of *Calanus* and other small planktonic organisms.

Barnes, H. & Bagenal, T. B. (1952). The habits and habitat of *Aporrhais pes-pelicani* (L.). *Proc. Malacol. Soc. Lond.* **29**, 101–105.

Heavy growths of sedentary organisms, particularly barnacles, were found on the shells of trawled specimens of *Aporrhais*, suggesting that this species, previously considered a burrowing form, spends much of its time on the surface of the mud. Young specimens, in which the 'lip' on the shell is not yet formed, do not bear these growths, suggesting that they live beneath the surface at this stage.

Booth, R. Haworth- (1952). Salmon mortality on the ebb tide. *Salm. Trout Mag.* **135**, 154–157.

An attempt on purely theoretical grounds to relate estuarial mortality of salmon to physiological factors which are held to be connected with the transfer from salt water to fresh.

Carruthers, J. N., Lawford, A. L., Veley, V. F. C. & Parrish, B. B. (1951). Variations in brood-strength in the North Sea haddock, in the light of relevant wind conditions. *Nature, Lond.* **168**, 317–319.

A survey of haddock brood-strengths from 1920 to 1949 suggests them to be at a maximum when local winds during spawning and post-spawning periods are favourable.

Cooper, L. H. N. (1952). The boar fish, *Capros aper* (L.), as a possible biological indicator of water movement. *J. Mar. Biol. Ass. U.K.* **31**, 351–362.

At certain times, large numbers of this species have been caught near the Eddystone. Their appearance may be correlated with 'submarine eagres' which might sweep shoals of the fish from their normal habitat, in canyons on the edge of the Continental Shelf, into the English Channel.

Crisp, D. J. & Molesworth, A. H. N. (1951). Habitat of *Balanus amphitrite* var. *denticulata* in Britain. *Nature, Lond.*, **167**, 489–490.

This variety of the barnacle has only been found in waters whose temperature has been artificially raised.

Duncan, A. (1952). A small colony of Grey Seals (*Halichoerus grypus* (Fabricius)) in the south of the Isle of Man. *Rep. Mar. Biol. Sta. Pt Erin*, **64** (1951), 22.

Observations were made on the colony from 1949 to 1952 and published records were examined. The Grey Seal is the usual seal in S. Manx waters and the only one to breed there. One specimen of the Ringed Seal, *Phoca hispida* Schreber, has been found. The size of the colony is estimated at about fifty animals. The numbers at the various points favoured by the seals vary seasonally. Breeding takes place from October to December, and a gathering occurs on the Calf of Man in March and April. Very few pups are produced by this colony.

Galliford, A. L. (1952). Notes on the fauna of shore pools near Red Rocks and Hilbre Point, Hoylake, and a suggested definition of the term 'brackish water'. *Proc. Lpool Nat. Fld Cl.* **1951**, 15–18.

A number of pools separated from the tidal water of the Dee estuary by a range of sand-hills have hitherto been regarded as brackish. Samples of water from them proved on analysis to have always less than 0·18 % salinity, and Rotifera, Cladocera and other animals were all typical of fresh water. It is suggested that 'brackish water' might usefully be defined as 'naturally occurring water' resulting usually from a mixture of sea water and fresh water and containing as a rule not less than 0·20 % NaCl.

'Green Parson' (1952). How far and fast can salmon travel? *Salm. Trout Mag.* **135**, 146–153.

A résumé of recent salmon tagging experiments in the British Isles and Scandinavia.

Harding, J. P., Marshall, S. M. & Orr, A. P. (1951). Time of egg-laying of the planktonic copepod *Calanus*. *Nature, Lond.* **167**, 953.

Mainly between midnight and 3 a.m.

Haslett, A. W. (1952). Research report. *Sci. News*, **26**, 113–122.

Reports under the sectional heading 'Sandhopper's compass' (pp. 121–122) the experiments of L. Pardi and F. Papi on *Talitrus saltator* at Naples which indicate that this sandhopper can orientate itself with reference to the polarization of light; populations normally employ this faculty in moving towards the sea.

Jones, E. W. Knight- (1952). Reproduction of oysters in the rivers Crouch and Roach, Essex, during 1947, 1948 and 1949. *Fish. Invest., Lond.* (Ser. II) **18** (2), 1–48.

In a group of shallow, warm, fully saline creeks the tidal movements may carry larvae considerable distances, but few are swept out to sea. Nannoplanktonic flagellates form a large part of the diet of the larvae, and are usually at between 5 and 10/mm.^{3} during fine weather. Routine plankton samples pumped in the area show peaks of abundance of newly liberated larvae at neap tides, i.e. spawning occurs at springs. Planktonic stages are completed within a week at 22–23° C., taking over eleven days at 17–18° C. Between 5 and 8% of the larvae produced in a season survive to metamorphose. The settling spat suffers severely from competition by other sessile organisms, of which the barnacle, *Elminius modestus*, is the most serious, while the Bryozoan *Membranipora lacroixii* may smother the small oysters. Artificial collectors of spat were more successful on bare mud than when placed near oyster stocks, the settling of the barnacles being less intense over mud. The influences of weather, competition, predation and food supply are discussed, and the possibility of the use of fertilizers is adumbrated.

MacDonald, R. & McMillan, N. F. (1951). The natural history of Lough Foyle, North Ireland. *Proc. R. Irish Acad.* **54** (B), 67–96.

Species lists and collecting stations for the Coelenterata, Mollusca, Bryozoa, Echinodermata, Porifera, and Arthropoda, and for the plankton. Short notes on some of the species, and on the brackish water fauna.

Matheson, C. (1950). Longevity in the Grey Seal. *Nature, Lond.* **166**, 73–74.

Record of a captive seal living twenty-six years and three months.

Orton, J. H. (1950). Recent breeding phenomena in the American slipper limpet, *Crepidula fornicata*. *Nature, Lond.* **165**, 433–434.

An apparently natural drop in spatfall occurred in 1945 for the first time on record. Breeding habits are described.

Quayle, D. B. (1951). Structure and biology of the larva and spat of *Venerupis pullastra* (Montagu). *Trans. Roy. Soc. Edinb.* (B) **62**, 255–297.

Contains information on seasonal fluctuations and vertical distribution of larvae in the plankton, and on settlement on experimental plates placed at different angles to the vertical. The distribution and survival of spat on a sandy beach during two years is recorded, and an attempt is made to correlate changes with environmental conditions.

Rees, W. J. (1952). Octopuses in the Channel. *New Biol.* **12**, 58–67.

A popular account of observations of the distribution, numerical fluctuations and probable lines of dispersal from breeding grounds off the north French coast. (See Rees, W. J. (1950), *J. Mar. Biol. Ass. U.K.* **29**, 361–378.)

Richardson, I. D. (1952). Some reactions of pelagic fish to light as recorded by echo-sounding. *Fish. Invest., Lond.* (Ser. II) **18** (1), 1–20.

Echo-sounder tracings of shoals of sprats in the Thames estuary, and of herring on various grounds in the North Sea, show that the fish shoal closer to the surface between sunset and sunrise than during daylight hours. Correlation of echo-soundings and Secchi disk readings by day show that the fish, whether feeding or no, are normally closer to the surface in turbid water, and differences in turbidity induce minor modifications in the behaviour of herring in different waters. Contrary to current theories, no evidence could be found of East Anglian herring lying close to the bottom and making brief, rapid 'swims' towards the surface. The use of searchlights shone vertically on to shoals at night demonstrates an immediate movement of the fish downwards, followed by an equally rapid rise when the light is switched off. Pilchard shoals show an immediate downward movement when so illuminated, but within a few minutes the fish rise well up towards, and even on to, the surface. Many small fish, e.g. sand-eels, young whiting and pollack fry, appear to move towards the surface, collecting in the illuminated area.

Stephenson, W. (1951). The Lesser Rorqual in British waters. *Rep. Dove Mar. Lab.* (3) **12** (1949), 7–48.

Statistical details of *Balaenoptera acutorostrata* have been obtained from published records of stranded whales, published records of foetuses, and data on catches within 100 miles of the British coast in 1945, 1946 and 1948. It appears that specimens are commoner in summer than in winter, that young are born between August and March with a maximum in November and December, and that newly born young are about 9 ft. long. The length frequency curve of stranded whales is trimodal; these modes may represent age groups. Ages as estimated from the baleen, however, are greater than those estimated from size segregation. Both modal length and maximal length are greater in females than in males. Off the English coast whales were feeding on herring and mackerel. The stomachs were often infested with the nematode *Anisakis simplex*.

Vevers, H. G. (1952). A photographic survey of certain areas of sea floor near Plymouth. *J. Mar. Biol. Ass. U.K.* **31**, 215–222.

Using an improved underwater photographic apparatus a quantitative survey has been made of two areas near Plymouth where dense populations of *Ophiothrix fragilis* occur.

Wells, G. P. (1951). On the behaviour of *Sabella*. *Proc. Roy. Soc.* (B) **138**, 278–299.

Describes experiments demonstrating the varying patterns of water currents through the tubes of *Sabella spallanzanii* and *S. pavonina*, and their relationship to respiration and feeding.

Wieser, W. (1951). Untersuchungen über die algenbewohnende Mikrofauna mariner Hartböden. I. Zur Oekologie und Systematik der Nematodenfauna von Plymouth. *Österr. Zool. Z.* **3**, 425–480.

An account of the ecology and taxonomy of free-living nematodes inhabiting various algae. Seventy species are listed, and descriptions are given of three new genera, eleven new species and one new variety.

Wieser, W. (1952). Investigations on the microfauna inhabiting seaweeds on rocky coasts. IV. Studies on the vertical distribution of the fauna inhabiting seaweeds below the Plymouth Laboratory. *J. Mar. Biol. Ass. U.K.* **31**, 145–174.

A detailed account, with species lists, of the rich fauna inhabiting intertidal seaweeds. Results are expressed quantitatively, as numbers of organisms per gram of weed. Three critical zones in the vertical distribution of species on the shore are recognized. Some species appear to have a different distribution at high and at low water.

Williamson, D. I. (1951). On the mating and breeding of some semi-terrestrial Amphipods. *Rep. Dove Mar. Lab.* (3) **12** (1949), 49–62.

Mating and egglaying in the Talitrids *Orchestia gammarella*, *O. mediterranea*, *Talorchestia deshayesii*, *T. brito*, and *Talitrus saltator* are described and compared with accounts published for the aquatic Gammarids. Probably because of the different habitat, carrying of the female by the male is modified and of less duration than among the Gammarids. Pairing does not take place until the female moults, and the time of egg-laying depends on the moult rather than on the time of copulation. The eggs are fertilized in the brood pouch, the spermatozoa remaining inactive until the eggs are laid.

Wilson, D. P. (1952). The influence of the nature of the substratum on the metamorphosis of the larvae of marine animals, especially the larvae of *Ophelia bicornis* Savigny. *Ann. Inst. Océanogr. Monaco*, **27**, 49–156.

Reviews the literature on larval settlement—some species can postpone metamorphosis for a period of time during which they can select a suitable substratum on which to settle. Experiments on the larvae of the polychaete *Ophelia bicornis* show that clean sands, of a suitable grade, are favoured, and that sands may be repellent to the larvae by virtue of a coating of organic matter or of living micro-organisms on the grains.

Wilson, D. P. (1953). The settlement of *Ophelia bicornis* Savigny larvae. The 1951 experiments. *J. Mar. Biol. Ass. U.K.* **31**, 413–438.

Experiments on settlement of larvae of this polychaete show that sands may be classed as attractive, neutral, or repellent to the larvae, and that the presence or absence of an organic coating on the sand grains seems to play an important part in rendering a sand repellent or attractive.

Wilson, D. P. & Armstrong, F. A. J. (1952). Further experiments on biological differences between natural sea waters. *J. Mar. Biol. Ass. U.K.* **31**, 335–349.

Water from the Firth of Clyde was found to yield better cultures of *Echinus esculentus* larvae than water from the English Channel. Results from mixing the two waters suggest that Channel water is deficient in some substance, necessary for normal development, which is present in Clyde water.

(*b*) Fresh Water

Bensley, C. J. F. (1952). The fresh water mollusca of Bookham Common. *Lond. Nat.* **31**, 34–39.

Monthly counts of molluscs in a pond that had been almost dry from August 1947 till December 1948 were made during 1950–51, and the numbers of each of five Gastropods are tabulated and shown in a graph. In 1946–47, *Planorbis planorbis* had in general been dominant, but in 1950–51, *Limnaea peregra* was the commonest, followed by *P. planorbis*; *L. palustris* showed an accountable decline, and one Gastropod not previously present was found. Counts in different habitats indicated that dead *Sparganium ramosum* was the most reliable throughout the year, the sluice wall was the most highly populated habitat in winter, and *Juncus effusus* was always poor. In general, no specific preferences were shown. The rapidity with which the pond became repopulated and the scarcity of new species indicated that the present population is derived from survivors of the earlier one. The number of molluscs and of species present in ditches and streams both greatly decreased following clearing. Two additional land molluscs are recorded for the area.

Butcher, R. W. (1952). Life and death in a river. *Trans. Lincs. Nat. Union*, **13**, 14–25.

A general sketch of the ecology of a river, with special reference to pollution.

Chen, Y. T. (1950). Investigations of the biology of *Peranema trichophorum* (Eugleninae). *Quart. J. Micr. Sci.* **91**, 279–308.

Cultures of the flagellate, *Peranema*, were maintained on a variety of substances, including live yeast cells, egg-yolk, milk and *Euglena* spp. and other unicellular algae. The feeding habits and methods of ingestion were observed; small organisms were swallowed whole, and larger ones engulfed or cut open and their contents sucked out. Gliding and swimming movements are described.

Fox, H. Munro (1950). The blood of water fleas. *Sci. News*, **15**, 86–104.

A popular summary, with ecological implications, mainly based on the author's own work on respiratory pigments, and referring especially to *Daphnia*.

Fox, H. Munro, Gilchrist, B. M. & Phear, E. A. (1951). Functions of haemoglobin in *Daphnia*. *Proc. Roy. Soc.* (B) **130**, 514–528.

Reviews the occurrence of haemoglobin in Crustacea. In four species of *Daphnia* a manifold increase of blood haemoglobin results from oxygen deficiency in the medium. It is shown that this additional haemoglobin increases length of life, enables more food to be gathered, allows more energetic movement, and increases egg production. Additional haemoglobin passed to the eggs accelerates embryonic development.

Gray, E. (1951). *Stylonichia mytilus* and the lunar periods. *Nature, Lond.* **167**, 38.

Demonstration by observation and statistical treatment of fluctuations in numbers of *Stylonichia mytilus* four to seven days before and after full moon.

Hannan, N. T. (1953). Locomotion in fishes. *Salm. Trout Mag.* **138**, 159–169.

'A new hypothesis' is presented to explain the mechanics of fish swimming. A somewhat incomplete and superficial treatment of a subject already fully dealt with by Gray, Harris and others.

Hardisty, M. W. (1951). Duration of the larval period in the brook lamprey (*Lampetra planeri*). *Nature, Lond.* **167**, 38–39.

Larval period exceeds five years, with 20–30 mm. increase in length each year.

Hawkes, H. A. (1952). The ecology of *Anisopus fenestralis* Scop. (Diptera) in sewage bacteria beds. *Ann. Appl. Biol.* **39**, 181–192.

The relative abundance, seasonal incidence and vertical and horizontal distribution of larvae of this sewage fly in the beds are determined by food supply, the size of the population in its turn affecting the subsequent food supply. Trapping of adult flies, as a means of estimating population, was abandoned in favour of removal of known samples from the beds at different depths and counting the larvae and pupae contained in them. The density of larvae decreased with increasing depth and was greatest below the jets. Pupae occurred in the same depth distribution pattern as did the larvae, but were normally found between, and not below, the jets. There is therefore no vertical migration, but some lateral migration, associated with pupation. The eggs are laid between the jets. Periodic rhythm in the population is considered to be related to irregularities in annual temperature changes.

Henderson, J. (1952). Notes on the genus *Ecdyonurus*. *Salm. Trout Mag.* **134**, 56–58.

A brief account of the characters and habits of *Ecdyonurus venosus*, *E. dispar* and *E. insignis*.

Huntsman, H. G. (1952). Wandering versus homing in salmon. *Salm. Trout Mag.* **136**, 185–191.

Evidence from the Moser, Margaree and Cheticamp rivers supports the opinion that return of salmon to fresh water is governed mainly by random wandering movements upon which may be super-imposed true 'homing' behaviour of purely local extent.

Johnson, R. S. (1953). Early and late running salmon. *Salm. Trout Mag.* **138**, 135–140.

A critical review of an earlier article by D. Sedgwick (1953, *Salm. Trout Mag.* **137**, 77–82) concerning the factors governing 'running habit' in salmon. It is concluded that in the relatively short rivers of the British Isles, which are so largely dominated by climatic conditions, segregation of spawners of different races is less likely than in the larger rivers of Canada and the U.S.A. There must therefore occur interbreeding which will, in the majority of cases, destroy at the outset the possibility of hereditary races.

Lowndes, A. G. (1952). Hydrogen ion concentration and the distribution of freshwater Entomostraca. *Ann. Mag. Nat. Hist.* (12) **5**, 58–65.

The pH ranges in which 176 species, mainly British, have been found, are given. Many can tolerate considerable variation.

Michael, P. (1952). 'Borderline fishes' of river and ocean. *Salm. Trout Mag.* **134**, 29–33.

An elementary description of the Cyclostomata with an account of British Petromyzontidae.

Mortimer, C. H. (1952). Water movements in lakes during summer stratification; evidence from the distribution of temperature in Windermere. (With an appendix by M. S. Longuet-Higgins.) *Phil. Trans.* (B) **236**, 355–404.

Gives a historical review of observations on internal seiches of lakes. Measurements with a thermo-electric thermometer (which is described) in Windermere confirm the findings of Wedderburn (1907–15) on Scottish lochs, showing that the 'temperature seiche' is a frequent feature of stratified lakes exposed to wind action. The movement is an important and largely unrecognized factor in studies of lake environments.

Popham, E. J. (1952). Notes on Corixid bionomics (Hemiptera Heteroptera). *Entomologist*, **85**, 73–77.

On submerged slopes in an aquarium, *Corixa distincta* faced in any direction with the angle of inclination differing from that of the substrate by 10° on slopes of 10–40°, settled horizontally or parallel to the substrate on slopes of 50°, and settled with head pointing downward on steeper slopes. Steepness of slope had little effect on the distribution of Corixids in a pond, though they were rare on reflex surfaces. *C. distincta* was most abundant where the pond bottom was of silt and decreased in numbers as the particles of which the bottom was composed increased in size. Experiments showed that at 22·5° C. *C. striata* is unlikely to migrate continuously for more than one hour and *C. nigrolineata* and *C. germari* for more than two; these species can probably travel 6–8 miles on a windless day. *C. punctata* and, to a less extent, *C. nigrolineata*, which commonly migrate, were more resistant to desiccation than *C. striata*, which can only be induced to migrate with difficulty.

Sedgwick, D. (1953). Early and late running salmon. *Salm. Trout Mag.* **137**, 77–82.

Little new information is brought to bear on the now well-worn controversy as to whether the 'running habit' in salmon is hereditary or governed purely by environmental factors.

Spurway, H. (1953). Territory and evolution in sticklebacks. *New Biol.* **14**, 33–43.

A critical discussion of Tinbergen's article (*New Biol.* **14**) pointing out that ethologists may be in danger of unconsciously adopting an anthropocentric attitude. Any other species of animal must have a picture of the external world which differs from that of man; this picture is an essential component in all the changes that, in sum, make up evolution.

Stewart, R. N. (1951). Icelandic char. *Salm. Trout Mag.* **133**, 239–244.

Field observations on the char which inhabit Icelandic rivers. Spawning habits, life history and migration of migratory subspecies appear similar to those of salmon though no smolt stage has been observed. Feeding (mainly on shrimp) continues into fresh water. Salmincolid parasites are described both as infesting migratory and non-migratory char.

Thornton, H. G. *et al.* (1952). A discussion on symbiosis involving micro-organisms. *Proc. Roy. Soc.* (B) **139**, 170–207.

Thornton and other contributors attempt to clarify the meaning and usage of the term symbiosis; a body of opinion prefers the original definition of the term by De Bary (1878), whilst the substitution of the term 'functional field' (Baker & Martin, 1937, 1938) is also supported. F. E. Fritsch contributes a short review of 'Algae in association with heterotrophic or holozoic organisms', referring to numerous animals associated with algae, indicating the range of associations known and showing that in all instances the relationship may be upset and change to parasitism of the alga by its partner. J. W. Howie and F. Baker contribute a paper on 'Rumen and caecal micro-organisms as symbionts' and T. Phillipson discusses 'The host in relation to alimentary micro-organisms'.

Went, A. E. J. (1952). Notes on Irish sea-trout. *Salm. Trout Mag.* **134**, 39–47.

Population studies of seatrout from various Irish rivers. Two- and three-year-old smolts largely predominate in roughly equal proportions. A majority return during the first post-migration year but more fish are mature after one winter at sea than in any other age-group. Approximately 20% of adults are previous spawners, some showing as many as five spawning marks. Smolt growth rates are inversely proportionate to age, but large 'river races' of smolts do not maintain their marked superiority in sea growth. Maximum recorded age and sea growth tend to be less than those recorded from other rivers in the British Isles.

White, J. H. (1951). Observations on the life history and biology of *Tipula lateralis* Meig. *Ann. Appl. Biol.* **38**, 847–858.

An account, with illustrations of egg, larvae and pupae, of the life cycle of a crane-fly from watercress beds in South Lincolnshire. The larvae feed principally on rotting submerged leaves, and do little damage to the beds. The life cycle may be completed in 63 days, and two, and probably a partial third, generations occur in the year.

'Yeoman' (1951). A note on caddis flies and their pupae. *Salm. Trout Mag.* **133**, 234–238.

A description of some common species of Trichoptera, their habits, metamorphosis and role as fish food.

(*c*) Land

Allison, J., Godwin, H. & Warren, S. H. (1952). Late-glacial deposits at Nazeing in the Lea valley, North London. (With a report on small Mammalia by M. A. C. Hinton.) *Phil. Trans.* (B) **236**, 169–240.

The deposits, whose sequences have been dated by pollen analysis and radio-carbon assay, are of special importance as bridging the time-gap between the 'Arctic-Plant Bed' of the Ponders End stage and the established Post-glacial sequence; they were formed in a shallow mere whose gradual drying up is reflected in faunistic and floristic changes. The succession of molluscan faunas is studied; the numerous species of small mammals include four of late Pleistocene character (with two species of *Lemmus*). Bones of *Bufo*, *Rana* and *Lacerta vivipara* were locally abundant. A general correlation for all the phenomena, geological, floristic and faunistic, relates them to corresponding phenomena in Britain and north-western Europe.

Andrewartha, H. G. (1952). Diapause in relation to the ecology of insects. *Biol. Rev.* **27**, 50–107.

A general account and classification assembling much material is given. The many different mechanisms and stimuli involved in facultative diapause are reviewed. Cytoplasmic maternal inheritance of the propensity is demonstrated. A theory which attributes diapause to the accumulation of 'intractable' stores of food materials in the tissues is put forward.

Arthur, D. R., Thompson, J. L. Cloudsley- & Sankey, J. H. P. (1951). Some aspects of the fauna of the district around Juniper Hall, Mickleham, Surrey. *Ent. Mon. Mag.* **87**, 275–278.

A miscellany of observations made during May 1951. In 'Rhythmicity in the wood louse *Armadillidium vulgare* Latr.', J. L. Cloudsley-Thomas (pp. 276–7) reports that counts by day and night showed this species to be most active during the morning. It was particularly numerous during sunshine, though there was no significant difference between numbers in shaded and more exposed areas. During a shower, it occurred only on protected, dry surfaces. The diurnal rhythm may be correlated with the positive phototaxis shown by certain individuals, especially after a rise in temperature. In 'The felled log as an ecological unit', D. R. Arthur and J. L. Cloudsley-Thompson (pp. 277–8) list the invertebrate macrofauna associated with felled logs in three woods, giving indications of abundance and habitats.

Banergee, S. N. & French, R. A. (1952). A note on the variability in the appearance of the brood in some British Lepidoptera. *Proc. R. Ent. Soc. Lond.* (A) **27**, 111–116.

The appearance and length of brood of seventeen species of nocturnal Lepidoptera have been studied for the periods 1933–36 and 1946–49.

Barnes, H. F. (1952). Studies of fluctuations in insect populations. XII. Further evidence of prolonged larval life in the wheat blossom midges. *Ann. Appl. Biol.* **39**, 370–373.

Contarinia tritici Kirby emerge, the majority, in the second year after the larvae have entered the ears; a few emerge in the same year, and some in the third year. Its parasites emerge after one or two winters. *Sitodiplosis mosellana* Géhin never emerges in the same year as the larva is in the ear. Usually most emerge after the first winter, but some may delay as long as twelve years. Its parasites continue emerging up to six years after collection of the larvae.

Barnes, H. F. (1952). Studies of fluctuations in insect populations. XIII. An improved method of ascertaining the correct date to sample when assessing larval infestations of the wheat blossom midges. *Ann. Appl. Biol.* **39**, 374–378.

Full-fed larvae of wheat blossom midges need moist conditions in order to descend to the soil. A dry spell at the full-fed stage causes accumulation of larvae and a mass descent when rain occurs. In wet conditions descent is gradual, since eggs are not all laid simultaneously. By taking 'pre-samples' of only five ears from a plot at regular intervals, several figures are obtained for the high numbers of larvae in the ears, and the time of descent of the larvae is revealed.

Barnes, H. F. (1953). The wheat blossom midges. *New Biol.* **14**, 82–103.

A condensed account of the author's long-term study of *Contarinia tritici* and *Sitodiplosis mosellana* at Rothamsted; deals with methods of study, life histories, population fluctuations and their causes, economic importance, prediction of outbreaks, and points out some outstanding problems.

Barnett, S. A., Bathard, A. H. & Spencer, M. M. (1951). Rat populations and control in two English villages. *Ann. Appl. Biol.* **38**, 444–463.

Censuses of rats were made at six-monthly intervals between spring 1947 and spring 1950 in two villages of south Devon, the census being taken either by test baiting or by census baiting, the latter proving the more reliable. In some instances one, two or three poison strikes were made after the census. Complete clearance was not achieved, and lasting reductions only occurred after comprehensive double or triple strikes, the rat population then taking over a year to recover. In each village the rats lived in discrete colonies, mostly in farms and chicken runs, infestation being encouraged by poor hygiene and dilapidation of cob and other buildings. *Mus musculus*, *Apodemus sylvaticus*, *Microtus agrestis*, *Clethrionomys glareolus* and *Sorex araneus* also visited the bait, as shown by the droppings, characteristic nibbling of grain, and by breakback trapping. Mouse activity increased after reduction of the rat population, but not necessarily because of increase of the mouse population. Total rat populations could not be estimated, but minimum numbers were 330 in one village of human population 266, in spring 1949, and 180 in the other, human population 364, in the autumn of 1948. The efficacy of control measures is discussed.

Boreham, H. J. (1951). Life history of the digger-wasp, *Mellinus arvensis*, Linn. *Trans. Suffolk Nat. Soc.* **7**, 98–107.

Observations on a colony in a man-made sandhill at Bury St Edmunds during August–October 1950, including the excavation of the nest-hole, methods of conveying prey and getting it into the nest-hole, variations in colour-markings, population, and a probable parasite.

Brown, E. S. (1951). Mimicry as illustrated in the British fauna. *New Biol.* **10**, 72–94.

Collates most of the available observations in respect of British insects, and illustrates a general account of mimicry with examples drawn from the British fauna.

Brown, G. (1951). The stone curlew, *Burhinus o. oedicnemus*. *Trans. Newbury Fld Cl.* **9** (2–4), 26–32.

A study of the breeding habits of the stone-curlew on one and a half square miles of downland, with notes on population density, habitat and nest sites.

Buck, F. D. (1951). Coleoptera in an owl's nest and its immediate environment. *Ent. Mon. Mag.* **87**, 274.

Lists of eleven species taken from a disused nest in an ash tree in Hertfordshire and four species from the wood mould beneath it.

Condry, W. M. (1952). Gors Goch Glan Teifi (Tregaron Bog). *Rep. W. Wales Fld Soc.* **14**, 17–19.

A general account of the fauna and flora of Tregaron Bog.

Cragg, J. B. (1950). Studies on *Lucilia* species (Diptera) under Danish conditions. *Ann. Appl. Biol.* **37**, 66–79.

Although the blowfly, *Lucilia sericata*, which is normally responsible for myiasis in sheep in Britain, occurs commonly in north-west Europe, outbreaks of myiasis are relatively infrequent there. In the Mols area of Denmark *L. sericata* was induced to oviposit on sheep by the use of chemical attractants. The relative humidity of the fleece, except during or immediately after rain, was never high enough to ensure hatching of the eggs. It is concluded that there is no evidence for the existence of a continental strain of the fly differing in oviposition habits from the British species.

Currie, P. W. E. (1952). The sawflies of the Cripplegate bombed sites. *Lond. Nat.* for 1951, **31**, 89–91.

The twelve species so far recorded are listed, with dates, food plants, localities and abundance. Several are sufficiently numerous to exert a significant effect on their food plants. No evidence of attack by parasites or predators has been found. The distribution of *Nematus pavidus* appears to be limited by the heat and dry conditions over most of the area, and these factors probably also limit the number of species present.

Eastop, V. F. (1951). Diurnal variation in the aerial density of Aphididae. *Proc. R. Ent. Soc. Lond.* (A) **26**, 129–134.

The diurnal variation of the aerial density of the twenty-two most abundant species of aphids in the summers of 1947–49 are given. Maximum densities were consistently obtained between 0900 and 2100 hr. G.M.T.

Edwards, E. E. & Evans, J. R. (1950). Observations on the biology of *Corymbites cupreus* F. (Coleoptera, Elateridae). *Ann. Appl. Biol.* **37**, 249–259.

Adults of this wireworm are on the wing in May and June in south Wales. Eggs are laid in June and incubation lasts about 34 days. The larva lives for about five years, pupating towards the end of July/beginning of August. Imagines emerge in about 21 days, and sometimes leave their earthen pupal chambers before the following spring. Larvae feed mainly on roots and underground stems, but can exist on decayed organic matter. They are eaten by birds (starling, blackbird, song-thrush, carrion crow recorded) and by carabid beetle larvae (*Pterostichus madidus, Nebria brevicollis, Harpalus rufi-cornis*). Parasites include a hymenopteran (unidentified) and fungi (*Metarrhizum anisopliae, Synglio-cladium cleoni*). Tarsonomid mites were frequently found in dead larvae from the field and from breeding pots.

Fraser, F. C. & King, J. E. (1950). Preliminary report on the bone remains from Star Carr, Seamer. *Proc. Prehist. Soc.* (N.S.) **15**, 67–69.

Examination of bones from this Yorkshire mesolithic site shows the presence of red deer (numerous—many of the antlers worked), roe deer (less abundant), elk (least common of the three, but important as providing substantial evidence of the occurrence of the species in England in Mesolithic times), bovid (undetermined), pig, badger, marten, fox, beaver and birds.

Fraser, F. C. & King, J. E. (1951). Second interim report on the animal remains from Star Carr, Seamer. *Proc. Prehist. Soc.* (N.S.) **16**, 124–129.

Appendix to a report by J. G. D. Clark on excavations on the mesolithic site at Star Carr. Mammals identified to date include red deer (the most numerous), roe, elk, oxen, pig, hare, beaver, marten, fox, badger and a canid which may be domestic dog. Birds include common crane, white stork, red-breasted merganser, red-throated diver, great crested grebe and little grebe. Antlers of red deer larger than, those of roe about same size as, modern British antlers. Two types of oxen present—a small race of *Bos primigenius*, and another type, probably the larger race of the same species. Most of beaver bones are of young animals. The general indications from conditions of antlers are consistent with human occupation of the site at all seasons of the year.

Golightly, W. H. (1952). Soil sampling for wheat-blossom midges. *Ann. Appl. Biol.* **39**, 379–384.

Soil samples taken to a depth of 6 in., with a 4 in. wireworm borer, were treated as for wireworm wet extraction, except that the float was not boiled, but washed back on to the large sixty-mesh sieve and spread evenly by a spray. Cocoons were easily seen and removed, the species being separated by colour. Twenty samples per field yielded statistically accurate estimates of numbers. Most larvae occur in the top 3 in., but considerable numbers occur down to 6 in. The headlands may carry fewer larvae than the rest of the field.

Green, A. A. (1951). The control of blowflies infesting slaughter-houses. I. Field observations of the habits of blowflies. *Ann. Appl. Biol.* **38**, 475–494.

Calliphora erythrocephala, *C. vomitoria*, *Lucilia caesar*, *L. illustris*, *L. sericata* and *Phormia terraenovae* are all pests of slaughter-houses, breeding profusely in the refuse. *Lucilia* is by far the commonest, especially *L. caesar*. *Musca* is commoner in the offices, canteens, etc., than in the slaughter-house proper. Extensive notes on the habits of different species in relation to weather, resting, reactions to light, preferences in feeding and oviposition, over-wintering behaviour and pupation migrations of larvae, with few statistical data. Discussion of control measures.

Green, J. (1951). The distribution of *Staphylinus ater* Gr. (Col., Staphylinidae) on Skokholm Island, Pembrokeshire. *Ent. Mon. Mag.* **87**, 106–107.

Staphylinus ater was confined to the upper part of the cliffs above the highest level of *Ligia oceanica*, did not occur under stones less than 1 ft. in diameter or at a steep angle and was frequently accompanied by *Abax parallelopipedus* or *Agonum ruficorne*. Its distribution on the island and that of six other species of *Staphylinus* are mapped.

Green, J. (1951). The cryptozoic Coleoptera of North Haven, Skokholm Island. *Ent. Mon. Mag.* **87**, 162–163.

A transect down a gully from cliff top (over eight ft.) to sea-level in July showed no clear zonation.

De Gryse, J. J. (1951). Forest entomology. *Sci. News*, **21**, 94–109.

Discusses, with examples and references, the ecological problems of forest entomology, especially in Canada.

Guild, W. J. McL. (1951). The Lumbricidae in upland areas.—I. Population variation in a small glen. *Ann. Mag. Nat. Hist.* (12) **4**, 653–657.

Nine species were found. No worms occurred in dry flinty soil, while the numbers from a flushed area were over twice as great as those from a drained acid peat area, which were themselves twice as great as an undrained area.

Guild, W. J. McL. (1952). The Lumbricidae in upland areas. II. Population variation on hill pasture. *Ann. Mag. Nat. Hist.* (12) **5**, 286–292.

Numbers in samples varied considerably in one pasture. Soil moisture, soil temperature and acidity are probably the most important limiting factors. Expressions like 'average earthworm field population' have no meaning.

Hacker, H. P. & Pearson, H. S. (1952). The growth, survival, wandering and variation of the long-tailed field mouse, *Apodemus sylvaticus*. III. Wandering powers and distribution. *Biometrika*, **39**, 389–413.

A population in Kent, living in a very varied habitat. An attempt is made to find out how much in-breeding is to be expected. Details are given of the distances between recaptures; 200 yards seems to be the normal maximum, but a definite statistic cannot be given because the figures are affected by the spacing of the traps, variation in size of area trapped and frequency of trapping, by seasonal and sexual variation in the mice, and the survival time after first capture. Of the habitats available only long grass was avoided. It is shown that the chance of close inbreeding was probably small.

Hafez, E. S. E. (1950). Sexual season of the ewe and daylight environment. *Nature, Lond.* **166**, 822–823.

A positive relation exists between the duration of the breeding season and the latitude and altitude of origin of the ewes of six breeds of sheep. Onset of season was variable but its mid-date coincided, except in the Dorset Horn, with the shortest day. Ovarian activity was shorter in ewe lambs.

Hafez, E. S. E. (1951). Inhibitory action of artificial light on the sexual season of the ewe. *Nature, Lond.* **168**, 336.

The effects on the oestrous cycle of artificially varying day-length are discussed.

Hafez, E. S. E. (1951). Sexual season in ewe lambs. *Nature, Lond.* **168**, 1046–1047.

Oestrous performance in ewe lambs is controlled by their growth-rate and the length of day.

Haggett, G. (1952). Observations on a colony of *Anepia irregularis* Hufnagel in Norfolk (Lep. Noctuidae). *Entomologist*, **85**, 36–38.

Contains some information on population density and parasitism in an isolated colony of this local moth.

Hall, D. W. (1951). Observations on the distribution, habits and life history of the bug, *Piezostethus galactinus* (Fieb.) (Hem., Anthocoridae). *Ent. Mon. Mag.* **87**, 45–52.

This Anthocorid, which normally occurs in such habitats as manure heaps, marshy places and under the bark of trees, was found in wheat and oats stored in bulk that was sprouting and heavily infested by *Laemophloeus ferrugineus* in Scotland. Field and laboratory studies showed that when the relative humidity of the air above the grain was 81 %, populations of *Laemophloeus* increased as the temperature increased above 60° F. with a maximum at 90–100° F., whereas populations of *Piezostethus* decreased as the temperature increased above 80° F. Increasing humidity favoured *Piezostethus* at temperatures up to 90° F. and *Laemophloeus* at temperatures of 80–106° F. Both insects died or migrated at 106° F. irrespective of humidity. Adults of *Piezostethus* preyed on larvae of *Laemophloeus*.

Haslett, A. W. (1950). Research report. *Sci. News*, **17**, 115–131.

Section on 'Climatic change' (pp. 122–123) briefly summarizes evidence bearing upon the amount and direction of current world-wide climatic changes. That on 'Sensory pits' (pp. 130–131) refers to recent work on the ability of crotaline snakes and of bees to detect infra-red radiation.

Haslett, A. W. (1950). Research report. *Sci. News*, **18**, 77–92.

Includes (pp. 90–92) a brief summary of studies by Lamb, H. H., on British weather types. These suggest that the year falls into five 'natural seasons' in Britain.

Haslett, A. W. (1950). Research report. *Sci. News*, **18**, 77–92.

Includes (pp. 77–82) popular review of recent work on the ability of arthropod eyes to detect polarization of light; includes some remarks of ecological importance.

Hincks, W. D., Shaw, S. & Steel, W. O. (1952). The entomology of Spurn Peninsula. *Naturalist*, 131–138, 169–176. (See also, 1951, *Naturalist*, 75–86, 139–146, 183–190.)

Continues the paper begun in 1951. Separate sections deal with the Coleoptera (excluding Carabidae and Staphylinidae), the Carabidae and the Staphylinidae.

Hooper, J. H. D., Hooper, W. M. & Shaw, T. R. (1951). Bat-banding in Devonshire. *Nature, Lond.* **167**, 555.

Of the 897 individuals, representing five species, ringed, 697 were greater horseshoe bats. These slept solitary or in groups of up to 300. Their hibernacula showed no sexual segregation. Flights occurred throughout the year and were frequently longer than one mile.

Howe, R. W. (1950). Studies on beetles of the family Ptinidae. III. A two-year study of the distribution and abundance of *Ptinus tectus* Boield. in a warehouse. *Bull. Ent. Res.* **41**, 371–394.

The beetle has two complete generations in a year; all stages may survive the winter. Methods for rapid estimation of numbers of *Ptinus* in a warehouse are discussed.

Howe, R. W. (1951). The movement of grain weevils through grain. *Bull. Ent. Res.* **42**, 125–134.

Calandra oryzae and *C. granaria* tend to move towards the bottom of a mass of grain; the movement is reduced in tightly packed grain, and is favoured by high moisture content, due to increased air-spaces. Weevils placed in the centre of a tight-packed mass of grain may be immobilized, but will lay eggs and be liable to initiate overheating.

Howe, R. W. (1951). Studies on beetles of the family Ptinidae. V. The oviposition rate of *Ptinus tectus* Boield. under natural conditions. *Bull. Ent. Res.* **42**, 445–453.

The oviposition rate depended on temperature, especially in winter, and on relative humidity, especially in summer. Darkness causes an increase in activity and in oviposition.

Howe, R. W. (1953). Studies on beetles of the family Ptinidae. VIII. The intrinsic rate of increase of some Ptinid beetles. *Ann. Appl. Biol.* **40**, 121–133.

Mainly a laboratory study of breeding rates under controlled temperature, humidity, food supply, etc., but with some observations on the conditions in warehouses, where various adverse factors induce a lower rate of increase of population, the mortality rate here being higher.

Howe, R. W. & Burges, H. D. (1952). Studies on beetles of the family Ptinidae. VII. The biology of five Ptinid species found in stored products. *Bull. Ent. Res.* **43**, 153–186.

Niptus hololeucus, *Trigonogenius globulus*, *Gibbium psylloides*, *Stethomezium squamosum* and *Eurostus hilleri* are studied with the object of estimating their potentialities as serious pests of stored products: it is concluded that none of the five is likely to become a pest, although all may exist as scavengers in warehouses. The literature on these species is surveyed.

Hueck, H. J. (1951). Influence of light upon the hatching of winter-eggs of the fruit tree red spider. *Nature, Lond.* **167**, 993–994.

A higher percentage of winter eggs of *Metatetranychus ulmi* hatch if kept in light than in dark. Light is believed to stimulate the advanced embryo to break the egg-shell.

Ibbotson, A. & Kennedy, J. S. (1951). Aggregation in *Aphis fabae* Scop. I. Aggregation on plants. *Ann. Appl. Biol.* **38**, 65–78.

Field observations on *Aphis fabae* on spindle and sugar beet show that the clustering of the insects within the boundaries of each leaf is due to active aggregation, as evidenced by size of aggregate relative to the leaf, distribution of individuals relative to leaf veins, the presence of more than one gynoparous individual in all but the smallest clumps, and the absence of single gynopara. In experiments in small leaf cages at least two gregarious reactions appear, the aphids probing more often and remaining inserted longer when near other insects. The selective value of the habit is discussed.

Johnson, C. G. (1952). The bedbug. *New Biol.* **13**, 80–97.

A general account of the life-history and biology of *Cimex lectuarius* in Britain, including a summary of some of the author's own studies on population ecology (see 1942, *J. Hyg., Camb.*, **41**, 345–461).

Johnson, C. G. (1952). The changing numbers of *Aphis fabae* Scop., flying at crop level, in relation to current weather and to the population on the crop. *Ann. Appl. Biol.* **39**, 525–547.

The numbers of *Aphis fabae* flying over bean and potato crops are estimated, using suction traps and correcting for wind speed where necessary. Climatic factors are measured with standard instruments as close to the crops as possible. Little flight occurs at night. By day, two peaks of flight occur, correlated possibly with flights (*a*) of winged forms moulted during the night, and (*b*) of those moulted during the day. Only very weak correlation is found between hourly flight densities and weather factors, especially wind speed. Most migration occurs in winds when the aphids can have no control over direction of flight, and the current view that migration only occurs in calm weather must be abandoned.

Johnson, C. G. & Eastop, V. F. (1951). Aphids captured in a Rothamsted suction trap, 5 ft. above ground level, from June to November, 1947. *Proc. R. Ent. Soc. Lond.* (A) **26**, 17–24.

Lists of the species and numbers of aphids captured in the trapping period. The occurrence of seasonal peaks is observed.

Johnson, C. G. & Penman, H. L. (1951). Relationship of aphid density to altitude. *Nature, Lond.* **168**, 337–338.

Tow-net and suction trapping of aphids was undertaken at intervals up to 2000 ft., in the early morning, at midday and in late afternoon. The results are considered in relation to phenological conditions.

Jones, G. D. Glynne- (1953). The honey-bee and agricultural chemicals. *New Biol.* **14**, 104–110.

Points out the increasing value of bees as pollinators with intensification of cropping, and the consequent danger of using chemicals to control insect pests. Discusses, with references, investigations proceeding, both in this country and elsewhere, of the toxicity of various insecticides to bees and the possible methods of using such chemicals whilst avoiding damage to bees.

Lancum, F. H. (1952). Game birds and agriculture. *Agriculture*, **59**, 287–289.

Discusses the significance of modern, enlightened game-keeping in conserving (indirectly) small birds, controlling crows, etc. Stresses the importance of wireworms, craneflies and slugs in the diet of pheasants, of weed seeds, injurious insects and slugs in that of partridges. Grouse, black and red, are of little concern to agriculturists, being rarely seen on cultivated lands.

Lancum, F. H. (1952). Home life of the badger. *Agriculture*, **59**, 435–440.

A brief report, from direct observations at setts, of some aspects of the badger's life. Emphasizes the importance of the sense of smell, and lists the results of supplying test foods on badger tracks.

Large, E. C. (1953). Thanks to the colorado beetle. *Agriculture*, **59**, 463–468.

Summarizes the first three reports of a European Plant Protection Organization working party reviewing plant importation and quarantine regulations in Europe. Discusses specific measures required in relation to the habits of different pests.

Leach, A. L. (1952). Some Caldey Caves. *Rep. W. Wales Fld Soc.* **14**, 8–12.

A brief geological account of the caves of the island with notes on Eel Point Caves, High Cliff Caves, and Nanna's Cave, and on the human and animal remains found in them. Shells of *Helix virgata* and *H. aspersa* regarded as Pleistocene and the earliest records for Wales.

Lees, A. D. (1950). Diapause and photoperiodism in the fruit tree red spider mite (*Metatetranychus ulmi* Koch). *Nature, Lond.* **166**, 874–875.

The environmental conditions of light and photoperiod in the larval development of females determine whether they shall ultimately lay 'winter' or 'summer' eggs. Summer eggs hatch soon after laying at 25° C., but winter eggs undergo a distinct diapause necessitating, optimally, a period of two hundred days at a temperature below 10° C.

Leston, D. (1952). Notes on the Hemiptera-Heteroptera of Bookham Common. *Lond. Nat.* **31**, 49–62.

The Heteroptera of the area are listed, giving months of capture and, for some, food plants and habitats, and the populations of aquatic species of a detritus pond on London clay that had been dry from September 1947 till December 1948 and for which topographical and vegetational details are given is discussed from data obtained in April and September 1951. Seventeen species were represented, but numbers were low; twelve were Corixids and five of these were breeding species. Numbers were highest in an area with dominant *Equisetum limosum*, plentiful *Glyceria* and *Sparganium erectum* and *Juncus effusus*, most species being in *Equisetum* and *Sparganium*, and low in one with shallow, clayey water, *Lemna trisulca* and a little *Glyceria* and *Juncus*. *Corixa moesta*, which was largely confined to submerged grasses and *Glyceria*, was dominant, and *C. sahlbergi* subdominant; their habitat preferences and that of *C. linnei*, which was also present, are discussed from the literature. The dark species, *C. moesta* and *C. sahlbergi*, were absent from a part of the pond with a light coloured bottom. The other Heteroptera included three species typical in southern England of ponds on clay with much vegetation and sloping muddy banks. A list of aquatic Coleoptera taken during the study is appended.

Matheson, C. (1953). Some aspects of urban zoology in Great Britain. *Sci. Mon., N.Y.* **76**, 29–32.

A survey of the interrelationships of man and some of the mammalian and insect species typically found in association with him in British cities.

Matthews, G. V. T. (1952). The problems of bird orientation. *Sci. News*, **23**, 46–60.

A discussion in the light of recent work, with references.

Meiklejohn, M. F. M. (1952). Habitat of chiffchaff in Scotland. *Scot. Nat.* **64**, 114–116.

There is a close connexion between the distribution of *Phylloscopus collybita* in Scotland and the presence of the rhododendron *Rhododendron ponticum*, which provides the only available cover when the bird arrives in early spring at a time when the weather is still cold and inclement. The editors suggest that the presence of suitable undergrowth cover in spring may be related to the distribution of several other warblers in spring.

Miles, M. (1950). Observations on the biology and control of cabbage root fly, *Erioischia brassicae* (Bché). *Ann. Appl. Biol.* **37**, 260–267.

Erioischia brassicae in south-east England begins egg-laying at the end of April, reaches a maximum by early May and continues to produce at a low level until early October. A few eggs are laid on Brassica plants, but the majority are found in the soil. Larvae occur continually from the end of April until mid-January, those in December and January being autumn hatched. They enter the soil after hatching and feed on, and later in, the roots of the plants. Great variation occurs in the size of puparia, the smaller ones being heavily parasitized by cynipid wasps. Comparative trials of control by calomel and benzyl hexachloride are discussed.

Miles, M. (1952). Further observations on the biology of the cabbage root fly. *Erioischia brassicae* Bché. *Ann. Appl. Biol.* **39**, 385–391.

Confirms earlier observations on egg laying. Although the reproductive capacity is about 100 eggs per female, with three to four generations per year, no increased infestation of plants occurs as the season advances. Large differences between observed populations of eggs and pupae indicate a heavy mortality rate among immature stages, and hence a high degree of natural control.

Owen, D. F. (1952). The Lepidoptera of Cripplegate. *Lond. Nat.* **31**, 84–88.

This preliminary survey contains a list of fourty-four species recorded from the City bombed sites, with notes on the habitats, habits, abundance, food plants, natural enemies and source of origin of fifteen. The upper soil layer of the area and its flora are in general favourable, especially to species affected by excessive dampness in winter, and a rapid increase in numbers followed by a slow decline, presumably as parasites arrive and build up, is characteristic. Parasitism appears to be the most important biotic limiting factor; predation by birds is negligible.

Perry, R. (1951). The life-history of the gannet. *New Biol.* **10**, 106–120.

Raw, F. (1951). The ecology of the garden chafer, *Phyllopertha horticola* (L.), with preliminary observations on control measures. *Bull. Ent. Res.* **42**, 605–646.

The beetle is more abundant in western counties, in grassland on light soils. The life-history is fully described, effects upon soil and vegetation and the efficacy of control by chemicals and by cultivation are discussed.

Rawle, S. G. (1951). The effects of high temperature on the common clothes moth, *Tineola bisselliella* (Humm.). *Bull. Ent. Res.* **42**, 29–40.

All stages of the moth were exposed to temperatures between 30 and 43° C. for varying periods, at R.H. 70%. 41° C. for four hours is lethal to all stages, the eggs being the most resistant. Complete development is possible at 33° C.

Ribbands, C. R. (1953). The inability of honeybees to communicate colours. *Brit. J. Anim. Behav.* **1**, 5–6.

Experimental demonstration of the inability of bees to communicate colours by dancing.

Richards, T. J. (1952). *Nemobius sylvestris* in S.E. Devon. *Entomologist*, **85**, 83–87, 108–111, 136–141, 161–166.

A detailed account of the life-cycle based on caged individuals, with information on distribution in Britain and Devon, habitat requirements, habits and food. Ten colonies in a limited area in S. Devon were all associated with oaks, and particularly with fallen oak leaves, which probably provide the best winter cover, though four were not in woods. Nymphs and adults appear to be omnivorous, but fungi probably form a substantial part of the diet; living insects were rarely attacked.

Robinson, H. S. (1952). On the behaviour of night-flying insects in the neighbourhood of a bright source of light. *Proc. R. Ent. Soc. Lond.* (A) **27**, 13–21.

The effects upon the natural population of insects over a given area from the introduction of a light trap are considered under the headings, repulsion, dazzle and inhibition.

Rooke, K. B. (1951). The effects of the cold spell (January to March, 1947). *Pap. Hampsh. Fld Cl.* **17**, 196–206.

Includes notes on birds found dead, causes of death, unusual movements, and a classified list of species affected.

Ryle, G. B. (1950). Forestry in South Wales. A generation of destruction and conservation. *Trans. Cardiff Nat. Soc.* **79**, 23–30.

An account of the history and present position of afforestation in South Wales, with notes on the associated animal life.

Smith, F. D. (1953). Farming against rabbits. *Agriculture*, **60**, 39–41.

Stresses the importance of rabbits as a symptom, rather than a cause, of dereliction, and hence of destroying burrows and cover. Notes that an empty, hungry, rabbit is more persistent in surmounting obstacles in order to reach food than is the full-fed animal on its way out again.

Spittle, R. J. (1951). The Coleopterous fauna of red squirrels' dreys. *Ent. Mon. Mag.* **87**, 184.

Two hundred and seventeen beetles, representing eighteen species and nine families, were obtained from eight dreys in coniferous trees in the New Forest during 1931–33. The species are listed and data given on the age and situations of the dreys.

Spurway, H. (1952). Can wild animals be kept in captivity? *New Biol.* **13**, 11–30.

Develops the thesis that any species of animal kept in captivity, in zoo, farm, or laboratory, is unavoidably subject to selection favouring departure from the wild type. Thus observations made upon captive animals are not necessarily applicable to populations of the same species but less influenced by man.

Swaine, G. (1951). Population studies on *Hylobius abietis* (L.) (Coleoptera, Curculionidae). *Ann. Appl. Biol.* **38**, 606–614.

Forty-year-old pines were felled in Bagshot Wood, Surrey, in October 1947, January 1948 and July 1948. Third-stage larvae were significantly more numerous in stumps of January 1948 felling, very few occurring in the October 1947 stumps, possibly because of the adversely drier environment they provided. Probably the January 1948 stumps contain more larvae than the July 1948 group because of longer exposure to ovipositing females. The roots, having a larger surface and food supply, support a larger population than the stump itself. Pupae sampled from June to August were almost as numerous as the third-stage larvae, indicating a low death-rate at this stage. No parasites were found. Populations of adults were followed using modified Grohmann traps baited with fresh pine logs covered with fresh pine brush. They rise rapidly to a peak in May as old beetles emerge from hibernation. Few are then found until a new generation emerges in mid-July. An attempt to estimate the population by Jackson's positive marking and recapture technique failed because used at a time when the population was increasing rapidly.

Thompson, H. V. (1953). The grazing behaviour of the wild rabbit, *Oryctolagus cuniculus* (L.). *Brit. J. Anim. Behav.* **1**, 16–19.

Discusses the economic effects of rabbit grazing on pastures, crops and young forest trees. Records behaviour while grazing, absence of individual sentries or of community spirit, periods of more intensive feeding in early morning and late evening, and evidence of feeding by night. Slight rain is no deterrent, but heavy rain and cold wind deter the animals, as do strong wind and snow. Damage to trees increases when snow is lying, but grazing on herbage has been observed on such occasions.

Thompson, J. L. Cloudsley- (1950). Economics of the 'Spotted Snake-Millipede', *Blaniulus guttulatus* (Bosc). *Ann. Mag. Nat. Hist.* (12) **3**, 1047–1057.

This species may attack crops in a dry spell following a period suitable for reproduction. Reproduction is favoured by dampness, humus, and lack of disturbance. Its activities in breaking down humus may be beneficial.

Thompson, J. L. Cloudsley- (1952). The behaviour of centipedes and millipedes. I. Responses to environmental stimuli. *Ann. Mag. Nat. Hist.* (12) **5**, 417–434.

Reactions to light, temperature, gravity, humidity and moisture, mechanical stimuli, and chemical stimuli. Diurnal rhythm. Most reactions are kinetic.

Thompson, J. L. Cloudsley- (1952). The relationship between reproductive rate and environmental resistance in British birds. *Ann. Mag. Nat. Hist.* (12) **5**, 990–1009.

Using data from *The Handbook of British Birds* (Witherby *et al.*, 1938–41), an attempt is made to show correlations between colour, powers of offence and defence, habits and habitats respectively and reproductive rate, and a correlation between sexual dimorphism and vulnerability (dimorphism of song or plumage being commoner in more vulnerable birds). The correlation between size and reproductive rate affects the calculations. This paper was written before Lack's papers on clutch size.

Thompson, J. L. Cloudsley- (1952). Millipedes in agriculture. *Sci. News*, **23**, 105–107.

Summarizes recent work by the author on *Blaniulus guttatus*.

Thompson, J. L. Cloudsley- (1953). Diurnal rhythms in animals. *Sci. News*, **28**, 76–98.

A general review of the subject; includes some examples from the British fauna.

Thompson, J. L. Cloudsley- (1953). A note on the littoral terrestrial arthropods of the Isle of Man. *Entomologist*, **86**, 11–12.

Includes lists of spiders and myriapods found near the shore, arthropods sheltering in tufts of lichen in the splash zone, and arthropods on a stone wall at night. There was some evidence of zoning from the splash zone to the top of the cliffs among woodlice. Recoveries of marked individuals of *Porcellio scaber* and *Oniscus asellus*, which were abundant on the wall, indicated that each remained there only for about half an hour, and that the total population was in consequence very large; they evidently did not crawl up from the ground, but emerged from holes in the wall. The centipede *Lithobius forficatus* is recorded preying on *Porcellio* for the first time.

Tinbergen, N. (1953). Fighting and threat in animals. *New Biol.* **14**, 9–24.

A general discussion, mainly concerned with interspecies fighting and threatening behaviour, their evolution and relationship to courtship display; exemplified by a number of British species, stickleback, herring gull, robin, etc.

Tribe, D. E. (1950). Influence of pregnancy and social facilitation on the behaviour of the grazing sheep. *Nature, Lond.* **166**, 74.

Social conditions of the environment and effects of pregnancy both influence time devoted to grazing of blackface ewes.

Vaughan, H. R. H. (1952). The Kite in 1951. *Rep. W. Wales Fld Soc.* **14**, 16–17.

In 1951 season young birds successfully brought to flying stage at six nests. The Field Committee were aware of eleven nesting pairs and had information suggesting that four more adult pairs probably exist.

Wardrop, J. C. (1953). Studies in the behaviour of dairy cows at pasture. *Brit. J. Anim. Behav.* **1**, 23–31.

Records continuous 24 hr. observations on ten Ayrshire cows in milk. The average times of grazing and cud-chewing were 7 and 16¼ hr. respectively, with 42% grazing time by day and 58% by night. Length and dampness of herbage and milk yield appeared to affect grazing time, and dryness and fibre content the period of cud-chewing. High temperatures by day caused periods of rest, most grazing being then in the cool of the early morning or late evening. Water was drunk on one, two or three occasions during the 24 hr.

Waterhouse, F. L. (1950). Humidity and temperature in grass microclimates with reference to insolation. *Nature, Lond.* **166**, 232–233.

A comparison of temperature and humidity between grass 60 cm. high and a recently cut lawn on a July afternoon.

Wilson, W. W. & Matheson, R. C. (1952). Bird migration and foot and mouth disease. *Agriculture*, **59**, 213–228 (available as separate at 4*d.*, by post 5*d.*, H.M. Stationery Office).

By critical analysis of major migratory movements of birds into and across Britain, concludes that there is a striking correlation between the seasonal incidence and location of primary outbreaks of foot-and-mouth disease in the south and east coastal areas of England and the autumn migration of birds from the Low Countries and the Pas de Calais. Correlative evidence is provided by the positive relation between major continental outbreaks and the incidence of primary strikes in Britain, as also by the identity of the strains in each case. On the evidence provided by the numbers of the various species of birds involved in the autumn migrations, and by their habits relative to pastures and to farm stock, the starling is indicated as the species most likely to be implicated. Experimental evidence is supplied establishing that birds can carry the virus for longer periods than those required for the sea passages from the Continent.

Woodroffe, G. E. (1951). A life-history study of *Endrosis lactella* (Schiff.) (Lep. Oecophoridae). *Bull. Ent. Res.* **41**, 749–760.

The white-shouldered house moth is widespread in Britain, and is a minor pest of stored products, especially of grain and seeds. The life-history and biology are described.

Woodroffe, G. E. (1953). Notes on some Hemiptera-Heteroptera from Hounslow Heath, Middlesex. *Entomologist*, **86**, 34–40.

An account of the topography and vegetation of the area with a fully annotated list of the more uncommon or interesting species, showing abundance and habitats and including a number of new county records, and a less detailed list of other species, based on visits during July–October 1952. A short list of beetles is also included.

Wright, D. W., Gearing, Q. A. & Dunn, J. A. (1951). Varietal differences in the susceptibility of peas to attack by the pea moth, *Laspeyresia nigricana* (Steph.). *Bull. Ent. Res.* **41**, 663–677.

Changes in the active moth population during the flight period were estimated, and also the proportion of this population to which the different pea varieties used had been exposed. There was strong positive correlation between the degree of exposure and the incidence of attack. Pea varieties providing the most dense cover (derived from estimate of average area of foliage per plant) suffered the heaviest attacks.

2. METHODS, APPARATUS, POPULATION STATISTICS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Anon. (1952). Under-water television. *Sci. News*, **25**, 91–96.

Sketches new apparatus suitable for viewing the sea-bed and marine animals.

Anon. (1953). Field centres. *Sci. News*, **27**, 93–96.

Report on the work of the Council for the Promotion of Field Studies, and brief descriptions of the centres established at Flatford Mill, Juniper Hall, Malham Tarn and Dale Fort.

Bailey, N. T. J. (1950). A simple stochastic epidemic. *Biometrika*, **37**, 193–202.

The case of a mild infection, with no infected individual removed by death, recovery or isolation. The curve of stochastic means differs from the deterministic curve and is more likely to resemble published returns.

Bailey, N. T. J. (1951). On estimating the size of mobile populations from recapture data. *Biometrika*, **38**, 293–306.

Discusses the precision of population estimates derived from simple recapture, Jackson's positive and negative methods, and from the triple-catch trellis. The author has summarized his conclusions in *J. Anim. Ecol.* **21**, 120–127 (1952).

Banks, C. J. (1952). An analysis of captures of Hemerobiidae and Chrysopidae in suction traps at Rothamsted, July 1949. *Proc. R. Ent. Soc. Lond.* (A) **27**, 45–53.

The daily captures of Neuroptera from a trap over beans and another over potatoes are given, together with the phenological conditions over the period of operation.

Barnes, H. (1952). Under-water television and marine biology. *Nature, Lond.* **169**, 477–479.

A note on the development of under-water television equipment at the Marine Station, Millport.

Barnes, H. F. (1950). The identity of the swede midge, with notes on its biology. *Ann. Appl. Biol.* **37**, 241–248.

The midge, *Contarinia nasturtii* Kieffer, which causes swollen and closed flowers on great watercress, *Rorippa amphibia*, in England, is shown by breeding and feeding experiments to be identical with midges which attack *R. amphibia* on the Continent and also damage rape, radish, turnip, swede and cabbage. Consequently, *C. torquens* de Meijere and *C. geisenheyneri* Rübsaamen must remain synonyms. Rearing experiments showed the presence of unisexual families.

Bateman, G. I. (1950). The power of the χ^2 index of dispersion test when Neyman's contagious distribution is the alternate hypothesis. *Biometrika*, **37**, 59–63.

Discusses the differentiation of Poisson and Neyman-contagious distributions, and the effect of population and parameter size on the needed sample or quadrat size. Tables and curves for testing the power of the index of dispersion test are given.

Benson, R. B. (1952). A new *Anoplonyx* destructive to larch in Britain (Hymenoptera: Tenthredinidae). *Bull. Ent. Res.* **43**, 543–547.

Describes *Anoplonyx destructor*, n.sp., a parthenogenetic sawfly recently recognized as destructive in Britain, where it is widespread. A key to the European species of the genus is included.

Blower, G. (1952). British millipedes with special reference to Yorkshire species. *Naturalist*, 145–157.

Summarizes the present knowledge of the Yorkshire Diplopod fauna. The comparatively few records for Yorkshire are placed against the background of the whole British millipede fauna. The paper includes notes on diagnosis, and a key to the British species, designed primarily for non-specialist workers in the field.

Boltz, C. L. (1951). Colour specification and measurement. *Sci. News*, **22**, 35–54.

Describes and evaluates different systems in use.

Brunner, A. Fraser- & Palmer, G. (1951). The Gadid Fishes of the Genus *Molva*. *Ann. Mag. Nat. Hist.* (12) **4**, 188–192.

Key to, and descriptions of, the three species of Ling, all of which occur off the west coast of Ireland.

Cameron, E. (1951). On the identity of an ichneumonid parasite of *Hepialus lupulinus* (L.). *Bull. Ent. Res.* **41**, 637.

The parasite described in the author's paper (1950, *Bull. Ent. Res.* **41**, 429–438; abstract in *J. Anim. Ecol.* **20**, 157) as *Alomya debellator* (F.) is now recognized as *Ichneumon suspiciosus* Wesm.; the systematic section of the earlier paper does not, therefore, apply.

China, W. E. (1951). Corrections to the check list of British Hemiptera-Homoptera. *Ent. Mon. Mag.* **87**, 280.

Collyer, E. (1951). The separation of *Conwentzia pineticola* End. from *Conwentzia psociformis* (Curt.) and notes on their biology. *Bull. Ent. Res.* **42**, 555–564.

Both species (Coniopterygidae, Neuroptera) are predators of the fruit tree red spider mite, and are recorded from Kent and Essex. The adults differ but slightly, but the immature stages are more easily distinguished.

Evans, G. O. (1952). British mites of the genus *Brachychthonius* Berl., 1910. *Ann. Mag. Nat. Hist.* (12) **5**, 227–239.

Key, descriptions and localities for the thirteen British species of this genus of soil and litter dwelling Oribatids, with drawings of eight species.

Finlayson, L. H. (1950). The biology of *Cephalonomia waterstoni* Gahan (Hym., Bethylidae), a parasite of *Laemophloeus* (Col., Cucujidae). *Bull. Ent. Res.* **41**, 79–97.

A full account of the life-history and biology, with a technique for laboratory culture, of the parasite. Several species of the host genus, which are pests of stored products, may be attacked. A tabular list of all bethylids known to attack insect pests of stored products is given.

Fisher, J. (1952). Bird numbers: a discussion of the breeding population of inland birds of England and Wales. *S. East. Nat.* **57**, 1–10.

Estimates of the breeding populations of inland birds of England and Wales, including a few based on actual or sample censuses, are shown to fit a log-normal frequency distribution, and not a simple logarithmic series.

Gauld, D. T. & Bagenal, T. B. (1951). A high-speed tow-net. *Nature, Lond.* **168**, 523.

A modified plankton net.

Goodey, J. B. (1952). The influence of the host on the dimensions of the plant parasitic nematode, *Ditylenchus destructor*. *Ann. Appl. Biol.* **39**, 468–474.

Random samples from eleven populations of *Ditylenchus destructor*, used in experimental transfers from various host plants to others, are analysed for size and dimensional ratios of the body and different organs. Significant differences are established in many cases, and the need for care in using dimensions as taxonomic data is stressed.

Grundy, P. M. (1951). The expected frequencies in a sample of an animal population in which the abundancies of species are log-normally distributed. Part I. *Biometrika*, **38**, 427–434.

Assumes that the counts for the different species are independent Poisson variates. Tables dealing with the case in which species are not represented in a sample, or are represented by one individual, are given.

Hinde, R. A. (1953). The term 'mimesis'. (With a reply by E. A. Armstrong.) *Brit. J. Anim. Behav.* **1**, 7–11.

A criticism of Armstrong's postulation of the term mimesis, by analysis of some of his examples of bird behaviour. Concludes that more exact information is required before the general postulate is accepted. Armstrong's answer maintains his position.

Howe, R. W. (1953). The rapid determination of the intrinsic rate of increase of an insect population. *Ann. Appl. Biol.* **40**, 134–151.

States and discusses, using specific examples from among insects, two modifications of the Leslie-Birch method of calculating the infinite rate of increase of any species. The first, by trial and error, divides the oviposition period into convenient unit periods; using a table of weighting factors, the calculated oviposition figures for all the unit periods are summed, to provide one figure which represents the observed egg number and pattern. For the second method, charts are provided, and the same table of weighting factors, from which may be represented the observed egg pattern of a constant rate of oviposition.

Howe, R. W. & Burges, H. D. (1951). Studies on beetles of the family Ptinidae. VI. The biology of *Ptinus fur* (L.) and *P. sexpunctatus* Panzer. *Bull. Ent. Res.* **42**, 499–511.

A modification by H. E. Hinton of S. M. Manton's key to larval Ptinidae, to include *P. sexpunctatus*, is appended.

Jackson, P. A. (1953). A simple type of fish counter. *Salm. Trout Mag.* **138**, 170–1.

A short factual account of a new type of counter. Migratory fish passing upstream are counted as they force their way through a grille of nylon threads, each under light spring tension, which are displaced sideways and in consequence close an electrical circuit which activates a recording voltmeter.

Johnson, C. G. (1950). A suction trap for small airborne insects which automatically segregates the catch into successive hourly samples. *Ann. Appl. Biol.* **37**, 80–91.

An electrically operated suction trap which takes in air at a constant rate in winds up to 12 m.p.h. and operates in all weathers, including heavy rain. Closely fitting disks fall into the collecting tube at hourly intervals so segregating successive hourly samples.

Johnson, C. G. (1950). The comparison of suction trap, sticky trap and tow-net for the quantitative sampling of small airborne insects. *Ann. Appl. Biol.* **37**, 268–285.

Experimental comparison of catches by suction trap, sticky trap and tow-net operating in different wind speeds. The sticky trap and tow-net, sampling by means of a variable wind from a changing population density, yield errors due to unknown weighting factors. The suction trap samples constantly in all wind speeds tested, as also in calm weather, when maximum numbers of insects may be in the air. The sticky trap may be attractive to some insects, for example, Psocoptera, Diptera and Hymenoptera, whereas the suction trap appears to sample by means of its air stream alone. The momentum of larger insects may account for the relatively greater catches of these by sticky traps.

Kapur, A. P. (1950). The biology and external morphology of the larvae of Epilachninae (Coleoptera, Coccinellidae). *Bull. Ent. Res.* **41**, 161–208.

Contains a description and figures of the larva of *Subcoccinella vigintiquator-punctata* (L.), the only phytophagous ladybird species known from Britain; adults and larvae feed on leguminous herbs.

Kettle, D. S. (1951). Some factors affecting the population density and flight range of insects. *Proc. R. Ent. Soc. Lond.* (A) **26**, 59–63.

The mathematical relationship between the extent of breeding site of an insect and the differences in population density at various distances from it are considered.

Kettle, D. S. & Lawson, J. W. H. (1952). The early stages of British biting midges, *Culicoides* Latreille (Diptera: Ceratopogonidae) and allied genera. *Bull. Ent. Res.* **43**, 421–467.

Keys to larvae and pupae of twenty-eight species of *Culicoides* found in Britain, and larvae and pupae of the genera *Stilobezzia*, *Serromyia* and *Ceratopogon*, including the subgenera *Ceratopogon* and *Isohelea*. Gives descriptions of larvae and pupae, including photographs of the fourth instars and figures of the 'hypopharynx' (the true epipharynx) of most of the larvae, with figures of the specific characters of the pupae. By analysis of the breeding preferences of *Culicoides* it is found that species can be placed in one of six groups depending on the larval habitat: (i) bog, (ii) fresh-water marsh, (iii) swamp, (iv) mud, (v) salt-water marsh, (vi) dung. The vertical distribution of seven species of *Culicoides* larvae is given, in the medium, the species differing markedly in this respect.

Leslie, P. H. (1952). The estimation of population parameters from data obtained by means of the capture-recapture method. II. The estimation of total numbers. *Biometrika*, **39**, 363–388.

If the death-rate is constant, an estimate of total numbers can be found, once the rate has been calculated, even if there is dilution of the population by birth or immigration. This estimate is probably slightly biased; a slightly different estimate, following Bailey's correction to the Lincoln Index, is reasonably unbiased. For a stochastic model, which is needed if a high proportion of the population is marked each time, the variances have to be increased, and an approximate formula is given. If there is no dilution the total numbers can be calculated directly, so the death rate may be variable. The difference in precision of grouping by marks or by time since last capture is negligible in this case. A better method is available if the death-rate is constant and there is no dilution; for this, grouping by time since last capture must be used. Numerical examples are given for these three cases. A possible solution to the general case in which there is dilution and a variable death rate, is put forward, but a large number of recaptures would be needed. A test for dilution is given, but this involves grouping by a third method, by time since first capture; if this test shows absence of dilution a less efficient estimate of total numbers can be got using the same grouping. A quick method of obtaining approximate estimates from a chain of samples covering several generations is demonstrated.

Leslie, P. H. & Chitty, D. (1951). The estimation of population parameters from data obtained by means of the capture-recapture method. I. The maximum likelihood equations for estimating the death rate. *Biometrika*, **38**, 269–292.

The estimation of the death-rate is a necessary first step in estimating the total population size. The death-rate is assumed to be constant over the sampling period and in all classes of the population, and a deterministic model of the recapture classes in the population after each sampling is constructed. The maximum likelihood equations for the death-rate, using all the information, are then found. A method of grouping the recaptures by the interval of time since they were last recaptured is shown to result in the loss of no information; grouping by the distribution of marks among the recaptures does lose information, but is more convenient if the proportion of recapture is low. A laboratory sampling experiment, using numbered disks, showed close agreement with theory, and also showed that the amount of information about the death rates increases rapidly with increasing numbers of samples.

Mann, K. H. (1952). Fresh water leeches. *Reading Nat.* **4**, 12–17.

Includes a key to British fresh-water leeches, with notes on collecting and on each individual species. *Trocheta subviridis*, an introduced species, is recorded from a lavatory in Reading.

Miles, M. (1952). Studies of British anthomyid flies. *Bull. Ent. Res.* **43**, 83–90.

This, the third paper in the series, deals with immature stages of *Delia cilicrura*, *D. trichodactyla*, *Erioischia brassicae*, *E. floralis* and *Pegohylemyia fugax*. They may cause damage to cruciferous crops, either separately or in mixed populations. Characters are given by means of which all immature stages of the several species can be distinguished.

Millidge, A. F. (1951). Key to the British genera of subfamily Erigoninae (Family Linyphiidae: Araneae): including the description of a new genus (*Jacksonella*). *Ann. Mag. Nat. Hist.* (12) **4**, 545–562.

Millidge, A. F. & Locket, G. H. (1952). New and rare British Spiders. *Proc. Linn. Soc. Lond.* **163**, 59–77.

Descriptions and illustrations of three spiders new to Britain, and of some species easily confused with each other. A large number of new county records is also given.

Moran, P. A. P. (1951). A mathematical theory of animal trapping. *Biometrika*, **38**, 307–311.

The estimation of the original population size from the diminishing number of animals killed in traps. Using the maximum likelihood method, equations are derived for the population size, the probability of catching an animal, and their standard errors. The method is unreliable if animals become trap-shy, if there is immigration, if the population is so large that there is no decrease in the number of animals caught, or if the probability of capture is not the same for each individual.

Moran, P. A. P. (1952). The estimation of death-rates from capture-mark-recapture sampling. *Biometrika*, **39**, 181–188.

Discusses points arising from Leslie and Chitty's paper (Biometrika, **38**, 269–292). In both the semi-probabilistic model of their sampling experiment and in a theoretical probabilistic model, the variance should be greater than that expected from the deterministic model. Further theoretical objections are advanced against the method of grouping the data used by Jackson and by Fisher and Ford. The method used by Leslie and Chitty is fully efficient in a deterministic model.

Nelder, J. A. (1952). Taking a sample. *Sci. News*, **24**, 107–114.

Introduction to statistical theory of sampling.

O'Rourke, F. J. (1950). The distribution and general ecology of the Irish Formicidae. *Proc. R. Irish Acad.* (B) **52**, 383–410.

Key to the Irish species. Swarming dates and altitudinal distribution are given where known.

Parry, D. A. (1951). Microclimate close to the ground. *Nature, Lond.* **167**, 73–74.

An indirect method of determining microclimatic conditions by measuring the temperature of a small black metal disk introduced into the microhabitat.

Perkins, J. F. (1952). On some British species of *Ichneumon* and *Alomyia* (Hym., Ichneumonidae). *Bull. Ent. Res.* **43**, 361–363.

Gives characters for distinguishing *I. suspiciosus* Wesmael from *I. septentrionalis* Holmgren and the subspecies *I. s. septentrionalis* and *I. s. scelestus* of the latter. Also gives characters distinguishing *Alomyia debellator* (F.) from *A. semiflavus* Stephens.

Quick, H. E. (1952). A key to the identification of the shells of the land snails of Reading area. *Reading Nat.* **4**, 1–10.

A useful illustrated key to the fifty-seven species of land snails (not slugs) that have been recorded for Berkshire.

Russell, F. S. (1950). Quantitative ecology of plankton. *Nature, Lond.* **165**, 559–560.

Value and methods of making quantitative assessments of planktonic organisms are discussed.

Skellam, J. G. (1951). Random dispersal in theoretical populations. *Biometrika*, **38**, 196–218.

The probability distribution of a population under random dispersal is deduced mathematically, and the result, which shows that the rate of radial expansion is constant, is applied to the spread of the British flora since the last glaciation, and of the musk-rat in Central Europe. This result is combined with various simple equations of population growth in which the density of the population, rather than the number of individuals, is used as a variable. Conditions for multiplication, stability and extinction in various types of habitats with different perimeter/area ratios are deduced. A law for population growth in a species with discrete generations is found, and this is used in studying two species in competition. It is shown that the species which is at a disadvantage in direct competition may be the survivor in a poor habitat but not in a rich one, if the reproductive capacity is sufficiently greater than that of the other species.

Skellam, J. G. (1952). Studies in statistical ecology. I. Spatial pattern. *Biometrika*, **39**, 346–362.

Several population models may produce the same distribution in quadrats. Three cases are discussed: (1) organisms randomly distributed with no interaction, (2) organisms in compact clusters which are smaller than the quadrat size, and (3) non-compact clusters much larger than the quadrats. The effect of variation in the habitat is considered. Six census distributions arise in several ways from these cases. The distance between neighbouring individuals, the comparison of pairs of quadrat readings and the use of quadrats of different sizes provide criteria for distinguishing the models. Cumulants and factorial cumulants are used in preference to moments in some of the calculations. The problem of the distribution to be expected in a population of annuals after several years is briefly dealt with.

Smith, K. G. V. (1952). The Irish Conopidae (Diptera). *Proc. R. Irish Acad.* (B) **54**, 203–208.

Key to all the British species. Status and distribution of the British species in Ireland.

Solomon, M. E. (1951). Control of humidity with potassium hydroxide, sulphuric acid and other solutions. *Bull. Ent. Res.* **42**, 543–554.

Amplifies and revises the well-known papers by Buxton (1931) and Buxton & Mellanby (1934). Methods of preparing solutions for accurate control of atmospheric R.H. are described, and some pitfalls in their use pointed out. Recent figures for humidities in contact with various saturated salt solutions are assembled and quoted.

Taylor, L. R. (1951). An improved suction trap for insects. *Ann. Appl. Biol.* **38**, 582–591.

Describes and illustrates modifications to the Johnson suction trap. Damage to insects caught is negligible at least in the case of aphids and lacewings.

Tebble, N. (1952). On three species of the genus *Ophelia* (Polychaeta) from British and adjacent waters. *Ann. Mag. Nat. Hist.* (12) **5**, 553–571.

Descriptions and figures of *Ophelia borealis*, *O. rathkei* and *O. roscoffensis*. These species have been regarded as synonyms of *O. limacina*, which does not occur in British waters. *O. borealis* is a northern and western form, *O. roscoffensis* occurs in the English Channel and the Bay of Biscay, and *O. rathkei* probably occurs in mud and sand all round the British Isles.

Thomas, M. (1951). Some tests for randomness in plant populations. *Biometrika*, **38**, 102–111.

Considers the problem of distinguishing between Poisson and double Poisson distributions in quadrats. Three tests are considered: Stevens's, which uses the number of quadrats with no individual, the index of dispersion, which compares the mean and variance of the sampling distribution, and a test based on the maximum likelihood of λ, the second parameter in the double Poisson distribution. The last is open to serious objection; the index of dispersion is probably the best of the three tests.

Turk, F. A. (1953). A synonymic catalogue of British Acari: Part I [Part II]. *Ann. Mag. Nat. Hist.* (12) **6**, 1–26, 81–99.

A check-list, with bibliography and with an index to subgenera and higher categories.

Turk, F. A. & Turk, S. M. (1952). Studies of Acari.—7th series: "Records and descriptions of mites new to the British fauna, together with short notes on the biology of sundry species." *Ann. Mag. Nat. Hist.* (12) **5**, 475–506.

Watson, H. & Verdcourt, B. (1953). The two British species of *Carychium*. *J. Conchol.* **23**, 306–324, pls. 9–10.

Distinguishing characters of two previously confused species of minute land snail, with account of habitats and distribution.

Williams, C. B. (1951). Changes in insect populations in the field in relation to preceding weather conditions. *Proc. Roy. Soc.* (B) **138**, 130–156.

Analysis of about 2850 nights' catches at a light trap at Harpenden. A high proportion of the mean change of total population can be accounted for by the effect of rainfall and minimum temperature in the three previous months; rainfall has a high positive effect in summer, but little or no effect in winter; minimum temperature has its lowest effect in summer. The method of analysis cannot be applied to single species of insects at present with any accuracy.

Williams, C. B. (1951). Comparing the efficiency of insect traps. *Bull. Ent. Res.* **42**, 513–517.

Catching with three different light traps is analysed, and large differences in their efficiency demonstrated.

Williamson, D. I. (1951). On the distinctive characters of *Orchestia mediterranea* da Costa and *Orchestia gammarella* (Pallas). *Rep. Dove Mar. Lab.* (3) **12**, 63–65.

The female of *Orchestia mediterranea* can be distinguished from the female of *O. gammarella* at all stages by the fact that in *O. mediterranea* the rami of each pleopod are as long as the peduncle. The whole limb is longer than in *O. gammarella*, in which the rami are only half as long as the peduncle.

Wolf, P. (1952). American problems and practice: V. Natural spawning or artificial production? *Salm. Trout Mag.* **134**, 9–15.

A survey of techniques of artificial spawning together with a factual account of experiments at Cultus Lake B.C. as a result of which it is concluded that artificial propagation, though slightly more efficient, under ideal conditions, than natural reproduction is uneconomical. Biological measures such as control of predators appear more promising.

Thomson, A. G. (1951). Control of insect populations. *Sci. News*, **20**, 58–63.

Briefly reviews, with references, some earlier and some recent studies of the natural factors regulating insect populations.

3. PARASITES

Arthur, D. R. (1950). The ticks of Glamorgan. *Trans. Cardiff Nat. Soc.* **79**, 9–22.

A full account of the economic importance and known distribution and hosts of five species of *Ixodes* known to occur in Glamorgan, with key, map, and diagram illustrating seasonal activity curve of *I. ricinus*—the most numerous species and the most important economically.

Arthur, D. R. (1953). Records of *Ixodes hexagonus* Leach from S.E. England and S. Wales (Acarina, Ixodidae). *Entomologist*, **86**, 76.

Numerous records of infestations on hedgehog, stoat, weasel, fox, badger, otter and polecat, mainly from south-east England and S. Wales, giving dates, localities, and number and developmental stage of the tick.

Baird, R. H., Bolster, G. C. & Cole, H. A. (1951). *Mytilicola intestinalis*, Steuer, in the European flat oyster (*Ostrea edulis*). *Nature, Lond.* **168**, 560.

Ten out of 248 oysters taken from Penryn River, Cornwall, and River Blackwater, Essex, were so parasitized.

Behura, B. K. (1950). A little-known tyroglyphoid mite, *Histiostoma polypori* (Oud.), and its association with the earwig, *Forficula auricularia* Linn. *Nature, Lond.* **165**, 1025–1026.

Bevan, W. J. & Edwards, E. E. (1951). Studies on the ox warble flies, *Hypoderma lineatum* and *Hypodermis bovis*. *Bull. Ent. Res.* **41**, 639–662.

Ecological studies of the seasonal activity, timing of the life-history and incidence on cattle in South Wales, related to topography and age of cattle. Reports experiments on effectiveness of control with DDT and BHC.

Cole, H. A. (1950). Shell disease in re-laid French oysters. *Nature, Lond.* **166**, 19–20.

The first records (1949) of shell disease in British oysters, due to the introduction of infected French individuals. Advanced infection is rare.

Cole, H. A. (1951). An *Odostomia* attacking oysters. *Nature, Lond.* **168**, 953–954.

Forty-six out of 100 oysters collected from the River Roach, Essex, in June 1951 were infested by *Odostomia*. The parasites generally occurred in pairs.

Crofton, H. D. (1952). The ecology of immature phases of trichostrongyle nematodes. IV. Larval populations on lowland pastures. *Parasitology*, **42**, 77–84.

Maximum population densities were reached between June and September, the time evidently depending more on specific conditions in each field than upon regional climatic conditions. On reseeded pastures relatively high populations were built up within the first season.

Crofton, H. D. & Thomas, R. J. (1951). A new species of *Nematodirus* in sheep. *Nature, Lond.* **168**, 559.

Outbreaks of nematode infection in the north of England in June and July 1951.

Fountain, H. C. (1951). Two cases of heavy infestation of small mammals by fleas and Acari. *Ent. Mon. Mag.* **87**, 1–2.

Lists of 1 anopluran and 4 acarines (including *Hirstionyssus isabellinus*, a first record for the British Isles) from a tame mouse and of 5 Siphonaptera and 5 acarines from a mole, both in Cornwall. The mites on the mole included hypopi of *Coelognathus putrescentiae*, which have been confused in the literature with those of *Acarus siro*, and distinguishing characters are given.

Freeman, R. B. (1953). Famous animals—5: The flea. *New Biol.* **14**, 111–124.

A general introduction to the Siphonaptera; life-history, host-distribution, parasites and enemies are considered.

Galliford, A. L. (1951). Notes on a parasite of the drinker moth. *Proc. Lpool Nat. Fld Cl.* 1950, 20–21.

Philudoria potatoria parasitized by the tachinid fly *Phryxe latilobata* in Cheshire.

Gilbert, O. (1951). Mites on bats. *Trans. Suffolk Nat. Soc.* **7**, 127.

Records of four species of mites on five species of bat, all from Suffolk.

Gilbert, O. (1951). Bats' parasitic Diptera. *Trans. Suffolk Nat. Soc.* **7**, 134.

Records of one species of Diptera and two species of flea on three species of bat.

Gillies, M. T. (1951). Association of a chironomid (Diptera) larva with *Ephemera danica* L. (Ephemeroptera). *Ent. Mon. Mag.* **87**, 200–201.

Of 120 nymphs from Hampshire examined in early April, nearly 60 % carried at least one larva of *Epoicocladius ephemerae*, 20 % carried two, and 8 % three or more. The larvae were present throughout March–August. They were not washed off by strong currents and pupated from June onwards in silt cocoons on the underside of the nymphs. They were frequent on mature nymphs and after the emergence of the subimagines migrated to a new host. Pupation occurs after the emergence period of the hosts, and mortality among drifting pupae is therefore avoided.

Gradwell, G. R. (1951). *Hebia flavipes* (R.-D.) (Dipt., Tachinidae), a parasite of the feathered thorn moth *Colotois pennaria* (L.) (Lep., Selidosemidae). *Ent. Mon. Mag.* **87**, 253.

Four adults emerged from a larva from Berkshire. This appears to constitute a new host record.

Green, J. (1950). Habits of the marine tardigrade, *Echiniscoides sigismundi*. *Nature, Lond.* **166**, 153–154.

Several collections of *Echiniscoides sigismundi* from the mantle cavity of the common mussel have been made.

Green, J. & Kingsbury, M. (1951). A Protozoan new to Britain parasitic in *Notiophilus* spp. (Col., Carabidae). *Ent. Mon. Mag.* **87**, 163.

Numerous sporonts of the Gregarine, *Actinocephalus notiophili* were taken in *Notiophilus biguttatus* and *N. rufipes* (a new host record) in Epping Forest in October 1949.

Green, J. & Wilkinson, W. (1951). Mites on insects of Skokholm Island. *Ent. Mon. Mag.* **87**, 143.

Observations in July 1950 indicated that on Skokholm gamasids are associated with cadavericoles and predators, uropodids mainly with stercoricoles, and red mites (probably erythracids) with insects that visit plants to feed. Gamasids appear to be carried to and about the island chiefly by *Necrophorus* spp. and may increase in numbers on beetles that are about to leave a corpse. *Necrophorus* spp. bore many gamasids, mostly on the head, thorax and elytra, whereas predaceous beetles, which visit corpses less frequently, carried only few.

Hassanein, M. H. (1951). Studies on the effect of infection with *Nosema apis* on the physiology of the queen honey-bee. *Quart. J. Micr. Sci.* **92**, 225–231.

The ultimate effect of infection with *Nosema apis* is to inhibit oviposition, culminating in the death of the queen. The eggs, larvae and pupae produced by infected queens were not infected by the parasite.

Hutton, R. F. (1953). *Cercaria reesi* n.sp., a new furcocercous larva from Plymouth. *J. Mar. Biol. Ass. U.K.* **31**, 581–585.

Description of a new species of parasite from the marine bivalves *Hiatella arctica* and *H. striata*.

Hutton, R. F. (1952). Studies on the parasites of *Cardium edule* L.: *Cercaria fulbrighti* n.sp., a *Gymnophallus* larva with a forked tail. *J. Mar. Biol. Ass. U.K.* **31**, 317–326.

Contains a list of trematode parasites which have been recorded from the cockle. *C. fulbrighti* differs from all previously described cercariae in that it loses its forked tail while still within the sporocyst.

Jackson, D. J. (1951). Nematodes infesting water beetles. *Ent. Mon. Mag.* **87**, 265–268.

Large numbers of small larval nematodes from the body cavity of three adults of *Hydroporus palustris*, *H. umbrosus* and *H. gyllenhali* collected in Fife in spring, larger larvae from an adult of *H. planus* collected in spring and a mature viviparous female from another collected in autumn, both from Hertfordshire, are tentatively determined as *Allantonema* sp. Their presence did not appear to affect the development of the wing muscles of the host. Very young Mermithid larvae were found in E. Fife, commonly under the elytra of *Agabus labiatus*, a very local and probably flightless colymbetine beetle, and rarely under those of *A. bipustulatus*, which is common and flies readily. They were not attached to their host and readily floated off. In *A. labiatus* as many as twenty-nine to thirty-seven were present on one host.

Kennedy, J. S. (1950). Aphid migration and the spread of plant viruses. *Nature, Lond.* **165**, 1024–1025.

Observations on the activity of *Myzus persicae* in relation to different plant species.

Lees, A. D. & Milne, A. (1951). The seasonal and diurnal activities of individual sheep ticks (*Ixodes ricinus* L.). *Parasitology*, **41**, 189–208.

Unfed ticks of known age were marked and their periods of activity were observed. 'The timing of the activity cycle appears to be largely determined by the availability of unfed ticks rather than by the prevailing meteorological conditions.'

Morley, C. (1950). A new parasite of the swallow-tailed butterfly. *Trans. Suffolk Nat. Soc.* **7**, 47–48.

Anagrus niveiscapus sp. nov. (Hymenoptera, Mymaridae) on eggs of *Papilio machaon* from Norfolk.

Naylor, E. (1952). On *Plagiostomum oyense* de Beauchamp, an epizoic turbellarian new to the British fauna. *Rep. Mar. Biol. Sta. Pt Erin*, **64** (1951), 15.

The Turbellarians, adults, cocoons and young, have been found on *Idotea* in Port Erin Bay. The Turbellarian, identified as *Plagiostomum oyense* de Beauchamp, is described in all stages. The hosts are *Idotea emarginata* and *I. neglecta*, the commonest local species, and the usual position of attachment is on the underside of the last thoracic segments. There is evidence that incidence of the Turbellarian increases with the size of the host in *I. emarginata*. It is suggested that the Turbellarian spends the whole of its life-cycle on *Idotea*.

Owen, D. F. (1953). Records of *Protocalliphora azurea* Fall. from bird's nests in Berkshire. *Ent. Rec.* **65**, 31–32.

Some twenty nests of great, coal and blue tits (*Parus major*, *P. ater* and *P. caeruleus*) each contained about twelve pupae in June 1952. The nestlings in general appeared unaffected and weighed about as much as those from uninfested nests, but one brood of great tits died when twelve days old, and their nest was found to contain about seventy pupae.

Parmenter, L. (1953). Some records of bred Tachinidae. *Ent. Rec.* **65**, 29–31.

A list of Tachinid flies bred mainly from lepidopterous larvae, with dates and localities, including a number of new host records.

Pike, R. B. (1953). The Bopyrid parasites of the Anomura from British and Irish waters. *J. Linn. Soc.* (*Zool.*), **42**, 219–237.

Lists twenty species, together with all their known localities and hosts. References to descriptions are given, and are supplemented by descriptions for some of the species. *Pleurcrypta marginata*, *P. strigosa*, *Athelges bilobus*, *A. prideauxii* and *Pseudione diogeni* are recorded for the first time in the British Isles. The parasites are not usually restricted to a single host species.

Rawson, D. (1952). The occurrence of parasitic worms in British freshwater fishes. *Ann. Mag. Nat. Hist.* (12) **5**, 877–887.

Records of about thirty species of parasites from thirteen species of fish, giving the number and location of the parasites, and the month and place of capture for each individual fish. Roach feeding on plants had no parasites. Parasites were generally commoner in the summer, and monogenetic trematodes were found only in July and August.

Smit, F. G. A. M. (1952). A possible explanation of the occurrence of the flea *Frontopsylla* (*Orfrontia*) *laeta* in Scotland. *Scot. Nat.* **64**, 74–83.

The species, known elsewhere only from Switzerland and the Caucasus, has now been reported from two east-coast Scottish counties. Three of the subgenera of *Frontopsylla* infest burrowing rodents, and the fourth (*Orfrontia*) lives on bird-hosts that nest in burrows or caves. *F. laeta* has been found only in nests of house-martins (*Delichon urbica*) on rocks or cliffs (never on buildings), and as at least one other member of the genus (*F. frontalis*) has been found in the nest of the Alpine chough (*Pyrrhocorax graculus*) it is conjectured that *F. laeta* could have been transferred from a mammalian host to *D. urbica* via the British chough (*P. pyrrhocorax*), which formerly nested on the east coast of Scotland in similar places to *D. urbica* and is known to use mammalian hair in the construction of its nest.

Smit, F. G. A. M. (1953). *Ctenophthalmus* (*Euctenophthalmus*) *congener congener* Roths., 1907: a flea new to Great Britain. *Entomologist*, **86**, 19–22.

On bank voles (*Clethrionomys glareolus*) in a wood in Hertfordshire.

Southward, A. J. (1951). On the occurrence in the Isle of Man of *Fecampia erythrocephala* Giard, a Platyhelminth parasite of crabs. *Rep. Mar. Biol. Sta. Pt Erin*, **63** (1950), 27.

The parasitic stage of *Fecampia erythrocephala* Giard was found in young *Carcinus maenas* from Port St Mary harbour. The infestation rate was 2%. The freeliving stage, which only lasted four hours, was observed, and is described together with an account of encystment.

Woodroffe, G. E. & Southgate, B. J. (1951). A common host and habitat of *Apanteles carpatus* Say (Hym., Braconidae) in Britain. *Ent. Mon. Mag.* **87**, 171.

The Ichneumonid, *Metacoelus mansuetor* and the Braconid, *Apanteles carpatus* were reared, respectively, from sixty and twenty-five mixed larval cultures of *Tinea columbariella* and *T. pellionella* originating from 122 nests of four bird species examined between August 1950 and March 1951. The data for *A. carpatus* are given, showing bird species, nest situation, locality and date.

4. FOOD AND FOOD HABITS

Barnett, S. A. (1951). Damage to wheat by enclosed populations of *Rattus norvegicus*. *J. Hyg., Camb.* **49**, 22–25.

Ten rats were introduced into each of four rooms containing sacked wheat and left there for 12–28 weeks. The value of the wheat eaten and the cost of cleaning the remainder were less than the cost of replacing the damaged sacks.

Behura, B. K. (1950). Note on the common European earwig, *Forficula auricularia* Linn. (Dermaptera) as food of the little owl, *Athene noctua vidalii* Brehm. *Ann. Mag. Nat. Hist.* (12) **3**, 775–776.

The life history of the earwig accounts for the proportions of males and females found in little owl pellets at different times of the year.

Bowers, A. B. & Williamson, D. I. (1951). Food of larval and early post-larval stages of autumn spawned herring in Manx waters. *Rep. Mar. Biol. Sta. Pt Erin*, **63** (1950), 17.

The food of larval and early post-larval herring taken to the east of the Isle of Man between September and December is described and compared with the available plankton. Larval herrings fed chiefly on mollusc veligers and also on small copepods: with the loss of the yolksac the importance of copepods increased, and above fifteen mm. *Pseudocalanus* sp. was the dominant food form. The percentage of feeding fish was higher in the post larvae than in the larvae. Most foods were taken according to the suitability of their size and their abundance in the plankton. The lack of diatoms in the larval diet contrasts with results from other areas.

Butler, C. G. (1951). The importance of perfume in the discovery of food by the worker honeybee (*Apis mellifera* L.). *Proc. Roy. Soc.* (B) **138**, 403–413.

Untrained scouting bees tend to associate some flower perfumes with food, whilst some flower perfumes do not attract. A new crop of strongly perfumed flowers will sometimes attract bees before they can see the flowers, though often it is necessary for a bee to approach very closely to a flower before discerning any perfume; attractive perfumes stimulate further exploration, whether the bee has learned to associate the perfume with food or not. These studies with untrained bees support those of von Frisch (1919) with trained bees.

Coles, M. D. (1951). Food relationships in freshwater. *Salm. Trout Mag.* **133**, 250–253.

An elementary and somewhat loosely written description of food chains in inland waters.

Crichton, M. (1951). Slugs feeding on mealybugs. *Ent. Mon. Mag.* **87**, 20.

Agriolimax laevis reduced populations of *Pseudococcus citri* on two species of plants in a glasshouse, where many mealybug colonies persisted on other plants. It has also been recorded feeding on mealybugs on glasshouse orchids, though slugs are not usually listed as predators of mealybugs.

Frost, W. E. (1952). Predators on the eggs of char in Windermere. *Salm. Trout Mag.* **136**, 192–196.

Char eggs, which appear to be unprotected by any form of redd, are preyed upon by many species of birds and fish, including the char themselves. Of the three types of char, winter lake-spawning, winter river-spawning and spring lake-spawning, the eggs of the first name are preyed upon by the common eel which was formerly considered quiescent during the period in question.

Gardner, A. E. (1953). Odonata and Hymenoptera with prey. *Entomologist*, **86**, 52.

Anax imperator and *Cordulia aenea* preyed on the Empid, *Hilara pilosa*, *Pyrrhosoma nymphula* on *Elater balteatus*, *Coenagrion pulchellum* on *Cloëon dipterus*, and *Erythromma najas* on *Sialis lutaria* in Surrey, and *Mellinus arvensis* on the Muscid, *Helina impuncta* in Norfolk.

Green, J. (1951). The food of *Cylindronotus laevioctostriatus* (Goeze) (Col., Tenebrionidae) and its larva. *Ent. Mon. Mag.* **87**, 19.

This beetle normally feeds on protococcoid algae on bark, but in the absence of trees on Skokholm fed on a lichen in which the associated alga is a protococcoid. The larvae appear to be somewhat indiscriminate feeders, generally associated with rotten wood and depending for nutriment on soluble products in the soil or wood.

Kennedy, J. S. (1951). Benefits to aphids from feeding on galled and virus-infected leaves. *Nature, Lond.* **168**, 825–826.

It was beneficial for *Aphis fabae* to feed on red-currant leaves infected with *Cryptomyzus ribis* and sugar beet with mosaic disease.

Kennedy, J. S. (1951). Aphids and plant growth. *New Biol.* **11**, 50–65.

Summarizes recent studies by the author of the distribution of host plants of *Myzus persicae* and *Aphis fabae*; discusses a theory of host plant alternation in terms of seasonal physiological changes in the plants.

Laurence, B. R. (1951). The prey of some tree trunk frequenting Empididae and Dolichopodidae (Dipt.). *Ent. Mon. Mag.* **87**, 166–169.

Insects preyed upon by *Tachypeza nubila* and five species of *Medeterus* on spruce during July–August 1950 are listed with dates and sex of prey and predator. Diptera, Psocoptera and Collembola formed the prey of *T. nubila* on seventy-nine, fourteen and eight occasions, respectively, and Thysanoptera, Diptera, Psocoptera, Collembola and arachnids that of *Medeterus* on thirty-eight, five, three, one and one, respectively. These data are briefly discussed, and observations on the feeding habits of the two genera are given.

Lockie, J. D. (1952). The food of great skuas on Hermaness, Unst, Shetland. *Scot. Nat.* **64**, 158–162.

During July and August 1950 the chief food of *Stercorarius skua* on the northernmost of the Shetland islands was juvenile kittiwakes, *Rissa tridactyla*. Two pairs of red-throated divers *Colymbus stellatus* nesting in the middle of the skua colony reared their young successfully.

Mendham, N. V. (1952). *Clausilia dubia* Draparnaud in curlew pellets. *J. Conchol.* **23**, 270.

A local species of land snail preyed upon by curlews.

Newstead, R. (1953). A spider and its prey. *Northw. Nat.* (N.S.), **1**, 94.

Saltica sp. attacking the moth *Lobophora carpinata*, which it had paralysed.

Salvage, S. (1951). Vegetable galls of the Eastbourne and Hailsham area. *Trans. Eastbourne Nat. Hist. Soc.* **13** (2), 3–8.

A list of host plants with the name of the galling agent and the position of the gall on the plant.

Tribe, D. E. (1952). Dietary self-selection experiments. *Sci. News*, **25**, 46–51.

Reviews work on rats and farm animals, shows that feeding behaviour is far from being an infallible guide to the nutritional requirements of these animals, and briefly discusses grassland management in the light of these results.

White, E. Barton (1953). Birds and butterflies. *Ent. Rec.* **65**, 55.

The prey of spotted flycatchers (*Muscicapa grisola*) in a garden included *Nymphalis io* (at rest), *Pararge aegeria*, *Maniola tithonus*, *Pieris rapae* or *napi*, and a Geometrid. *Pararge megera* was attempted but missed, and *Vanessa atalanta*, *Polygonus c-album* and *Polyommatus icarus* were ignored.

Woodroffe, G. E. & Southgate, B. J. (1951). An apparent association between certain Pentatomid and Coreid bugs and the seeds of their food plants. *Ent. Mon. Mag.* **87**, 308.

Notes are given on the occurrence of six Pentatomids and one Coreid that were confined almost exclusively to plants bearing ripening fruits, and the normal existence of a close correlation is suggested.

5. MIGRATION, DISPERSAL AND INTRODUCTIONS

Allen, A. A. & Lloyd, R. W. (1951). *Pyrrhidium sanguineum* L. (Col., Cerambycidae) as a British species. *Ent. Mon. Mag.* **87**, 157–158.

This beetle, which is recorded breeding in a native tree (oak) apparently for the first time in this country, is considered to be a relic of the indigenous fauna of the remnant of primary forest in Herefordshire in which it occurred. Notes on the bionomics are included.

Anon. (**1951**). Census of Essex heronries, 1950. *Rep. Essex Bird Watch. Soc.* **1950**, 5–6.

The population of *Ardea cinerea* in the county has decreased from 216 pairs in 1928 to 151 pairs in 1950. This is in spite of the fact that thirteen colonies were enumerated in 1950 and only six in 1928.

Anon. (**1952**). Summary of results of counts of brent geese on the coast and of duck on inland waters during the winter 1950–1951. *Rep. Essex Bird Watch. Soc.* **1951**, 32–34.

Counts of Anatidae in connexion with the national census organized by the Wildfowl Inquiry Committee. A maximum of 5000–6000 *Branta bernicla* on the coast, and of 6779 duck on all inland waters in Essex more than 20 miles from London; the overwhelming majority of the duck maximum (more than 99 %) were on a single reservoir at Abberton.

Atkinson, R. & Roberts, B. (**1952**). Notes on the islet of Gasker. *Scot. Nat.* **64**, 129–137.

A list of the breeding birds, with some population estimates, of a 47-acre islet off Harris, and some notes on the population of the grey seal, *Halichoerus grypus*.

Biggs, H. E. J. (**1951**). Diptera of East Anglia—some additions. *Ent. Mon. Mag.* **87**, 237–238.

A list, with dates and localities, including a number of additions for Norfolk and Suffolk.

Bilby, H. A. (**1950**). Ornithological report: Breeding bird census area, Harlington, Sept. 1st '48–Aug. 31st '49. *Quart. Rev. W. Middx Sci. Soc.*, Supp. no. 3, 14–18.

A census of breeding birds in an area of over 500 acres of farmland, orchards and houses with gardens in south-west Middlesex. There were thirty-two breeding species, of which twenty-one nested in the orchards.

Bilby, H. A. (**1950**). Swift and hirundine census, 1949. *Quart. Rev. W. Middx Sci. Soc.*, Supp. no. 3, 18–20.

A census of *Apus apus*, *Hirundo rustica* and *Delichon urbica* in 6¼ sq.m. of suburban and market-garden land in south-west Middlesex. Numbers of breeding and non-breeding pairs and number of young successfully hatched and fledged are given.

Blackie, J. E. H. (**1952**). Further notes on *Strymonidia pruni* L. *Entomologist*, **85**, 93–94.

The range in England is defined. The requisite conditions appear to be ancient forest and abundant *Prunus spinosa* on boulder clay at altitudes below 400 ft. with annual rainfall of 26–30 in. and an average annual mean temperature of about 48° F. The probable origin of the present distribution is discussed.

Blezard, E. (**1953**). The pond snail, *Limnaea stagnalis* (L.) in Cumberland. *Northw. Nat.* (N.S.) **1**, 95.

Recorded for Cumberland for the first time in 1948.

Blower, G. (**1953**). On three species of *Cylindroiulus* Verhoeff (Diplopoda, Iulidae) in Britain. *Ann. Mag. Nat. Hist.* (12) **6**, 305–316.

Synonymy, descriptions, figures, habitats and recorded distribution for *C. latestriatus* (=*C. owenii*), *C. parisiorum*, and *C. britannicus*.

Bradley, J. D. (**1952**). *Adoxophyes orana* (Fischer von Roeslerstamm, 1834) (Lepidoptera: Tortricidae). *Entomologist*, **85**, 1–4.

Contains characters for the identification of the adults of this recent addition to the British list, with notes on its seasonal life-history and feeding habits.

Bristowe, W. S. (**1952**). The spiders of islands. *S. East. Nat.* **57**, 34–43.

A general discussion, with special reference to the islands off the coasts of the British Isles.

Browne, F. Balfour- (**1951**). Additions to the list of the aquatic Coleoptera of Ireland. *Ent. Mon. Mag.* **87**, 260–264.

Additions for Clare, South and West Galway, Longford and Sligo, with some distributional notes.

Burton, M. (1950). The synonymy and distribution of *Myxilla fimbriata* (Bowerbank), with notes on other related species of sponges. *Ann. Mag. Nat. Hist.* (12) **3**, 888–892.

Myxilla fimbriata occurs on gravel, stoney, or rock bottoms from 55 to 710 m. in S.W. Ireland, N. Ireland, Orkney, Shetland, and Northumberland, and from Baffin Bay to the Barents Sea.

Carlisle, D. B. (1953). Notes on the British species of *Tridemnum* (Didemnidae, Ascidiacea), with a report of the occurrence of *T. niveum* (Giard) in the Plymouth area. *J. Mar. Biol. Ass. U.K.* **31**, 439–445.

The first definite record of *Tridemnum niveum* in British waters. At Roscoff it extends from a little below low-tide mark to about 30 m., and is especially abundant on the sargassids which inhabited the *Laminaria* zone.

Corbin, P. G. (1950). *Ammodytes immaculatus*, a new species of sand-eel found in European seas. *Nature, Lond.* **166**, 525–526.

Dale, W. S. & Hallett, H. M. (1950). Entomological notes: 1946–48. *Trans. Cardiff Nat. Soc.* **79**, 49–51.

Records of Lepidoptera, Odonata, Hymenoptera and Coleoptera, with a note of recently-published additions to the county list. Two new Coleoptera, *Plagionotus arcuatus* L., and *Saperda scalaris* L., probably imported with timber, added to the Glamorgan list.

Dannreuther, T. (1952). Migration records, 1951. *Entomologist*, **85**, 125–131, 155–160.

Includes summaries of the recorded abundance, range, movements and distribution in Britain of ten regular migrant butterflies and moths, records of butterflies, moths and a dragonfly at light vessels, of rarer vagrant and other moths in Britain, of other insect immigrants in Britain, and of migrations of butterflies, moths and dragonflies from Europe and North Africa.

Davis, A. G. (1952). *Truncatellina cylindrica* (Férussac) in Norfolk. *J. Conchol.* **23**, 269–270.

Habitat of a rare species of land snail near Thetford.

Duffey, E. (1953). On a Lycosid spider new to Britain and two rare spiders taken near Oxford. *Ann. Mag. Nat. Hist.* (12) **6**, 149–157.

Pirata uliginosus Thor. occurs in grassland and bracken near Oxford, on *Sphagnum* bogs in Germany and pond margins in Roumania. The common factor seems to be its restriction to the litter or the soil/litter interface. The habitats of *Zygiella stroemi* (conifer trunks) and *Oxyptila nigrita* (short grass on limestone) are also discussed.

Eason, E. H. (1951). Notes on the Chilopoda (Centipedes) of Warwickshire and Worcestershire. *Ann. Mag. Nat. Hist.* (12) **4**, 257–268.

Records for eighteen species, and the previously published records for these species from Nottinghamshire, Derbyshire and Staffordshire.

[Ellis, A. E.] (1951). Census of the distribution of British non-marine Mollusca. (7th edition.) *J. Conchol.* **23**, 171–244.

Summary of British and foreign distribution, earliest fossil occurrence, habitats, of native and introduced species. Distribution tables and maps.

Ellis, E. A. (1951). The introduction of the large copper butterfly, *Lycaena dispar batavus* (Oberthür), at Wheatfen Broad, Norfolk. *Trans. Norfolk Norw. Nat. Soc.* **17**, 84–89.

The Friesian race of the large copper having apparently become extinct in its native habitat during the recent war, and being threatened by drainage in its last surviving (introduced) locality in Huntingdonshire, it was decided to attempt to introduce it in a further locality, in the Yare valley in Norfolk. The 1949 and 1950 seasons were reasonably successful.

Evans, G. O. (1952). Terrestrial Acari new to Britain.—I. [II.] *Ann. Mag. Nat. Hist.* (12) **5**, 33–41, 660–675.

Thirty-six species of Oribatid mites new to Britain (eight new to science), mainly from coniferous and deciduous plantations in South Bedfordshire. The soil layer in which the species was found is given.

Fisher, J. (1951). Bird preservation. *Trans. Norfolk Norw. Nat. Soc.* **17**, 71–83.

Includes a general survey of the changes in status of British breeding birds since 1900.

Fraser, G. de C. (1951). Entomological Notes, 1950. *Proc. Lpool Nat. Fld Cl.* **1950**, 19–20.

Notes on Lepidoptera and Coleoptera in the Formby district of Lancashire, including *Heliothis armigera* (Lep.) believed to have been imported in tomatoes, and *Hadena chenopodii* (Lep.), which appears to have suddenly irrupted into the area. Attention is drawn to the danger of mercury vapour lamps to moths.

Fryer, G. (1951). Distribution of British freshwater Amphipoda. *Nature, Lond.* **168**, 435.

Records of *Eucrangonyx gracilis* and *Gammarus pulex* from Huddersfield-Ashton canal and *Orchestia bottae* from Huddersfield.

Galliford, A. L. (1950). Notes on the aquatic fauna and flora of Knowsley Park. *Proc. Lpool Nat. Fld Cl.* **1949**, 11–14.

A list of Rotifera and Cladocera collected in an artificial lake, White Man's Dam, and its associated ponds, in Lancashire. A comparison is given with another dam's algal flora to show the effect of industrial drainage. There is an analysis of the water for hardness.

Galliford, A. L. (1951). Preliminary notes on the microscopic aquatic fauna and flora of Bidston Moss. *Proc. Lpool Nat. Fld Cl.* **1950**, 15–18.

A list of Rotifera, Cladocera and Copepoda from ten stations on a moss in the Wirral Peninsula, Cheshire, viz. four ponds, one muddy ditch, two streams, two puddles in cart-ruts, and a brackish pool. The cart-ruts puddles were more productive of numbers, though not of species, than the ponds.

Gardner, A. E. (1953). Odonata and Orthoptera in Caernarvonshire. *Entomologist*, **86**, 8.

New county records for *Aeshna cyanea* and *Sympetrum danae* and confirmation of an old record of *A. juncea*.

Gauld, D. T. (1952). *Staurophora mertensii* Brandt in the Firth of Clyde. *Nature, Lond.* **169**, 752.

A note on the occurrence of this arctic leptomedusan in the Firth of Clyde in 1951.

Gibson, J. A. (1953). Observations on the breeding birds of Ailsa Craig in 1947. *Northw. Nat.* (N.S.) **1**, 18–22.

Two new colonies of gannets (*Sula bassana*) were established and the number of pairs increased from 4829 in 1942 to 5383. Twites (*Carduelis flavirostris*) and fulmars (*Fulmarus glacialis*) bred for the first time, meadow and rock pipits (*Anthus pratensis* and *A. spinoletta*) increased greatly in numbers, but hedge-sparrows (*Prunella modularis*), which normally breed, were absent. A preliminary count of auks showed the percentage of bridled guillemots to be just under one.

Green, J., Pearson, A. E. G. & Wilkinson, W. (1951). The Coleoptera of Skokholm Island. *Ent. Mon. Mag.* **87**, 196–199.

A preliminary list of species taken during 17 June–19 July 1950, with habitats, localities and abundance is given with some topographical information.

Haggett, G. (1952). *Rhodometra sacraria* (Lep. Geometridae) in Great Britain, with particular reference to its occurrence in West Sussex, 1947. *Entomologist*, **85**, 49–56.

Information on the occurrence in Great Britain during 1947–50, habitat requirements, migration, and bionomics under cage conditions.

Harrison, J. W. Heslop- (1947). The Pleistocene races of certain British insects and distributional overlapping. *Ent. Rec.* **59**, 141–145.

Discusses the occurrence and distribution of races of Lepidoptera, particularly *Aricia agestis*, which is related to the distribution of its food-plant the rockrose, *Helianthemum vulgare*, and of the humble bee, *Bombus smithianus*, the dragonfly, *Sympetrum striolatum*, and some Homoptera and Coleoptera. Concludes that the pattern of distribution, and of zones of hybridization, can be explained as a result of the survival of glaciation by Pleistocene stocks in north-western refuges and later the interbreeding of these stocks with others arriving in Britain in early Holocene times.

Harrison, J. W. Heslop- (1950). A dozen years' biogeographical researches in the Inner and Outer Hebrides. *Proc. Univ. Durham Phil. Soc.* **10**, 516–524.

Summarizes results of recent surveys of the fauna and flora of the Western Isles, and concludes from the biological evidence, and from peat remains, that eustatic and isostatic changes of land level during the glacial periods must have resulted in a high elevation of the land during part at least of this time, when the Hebrides must have formed a continuous land mass. The presence of a number of Irish species of plants and animals on Coll, Tiree and Gunna, and their exclusion from the Outer Hebrides, indicates the presence of a clear post-glacial land connexion between the Treshnish Islands and Ireland, which country is postulated as the main refuge of the relict species.

Harrison, J. W. Heslop- (1953). Lepidoptera in the Isles of Lewis and Harris in 1952. *Entomologist*, **86**, 53–55.

Includes some new records for the Shiant Isles.

Harrison, J. W. Heslop- & Morton, J. K. (1952). Lepidoptera in the Isles of Raasay, Rhum (v.-c. 104), Lewis, and Harris (v.-c. 110) in 1951. *Entomologist*, **85**, 6–13.

An annotated list, including several new records for individual islands and some information on status and habitats.

Higgins, L. G. (1950). A descriptive catalogue of the palaearctic *Euphydryas* (Lepidoptera: Rhopalocera). *Trans. R. Ent. Soc. Lond.* **101**, 435–489.

The only British species, *Euphydryas aurinia aurinia*, occurs in local colonies in most parts of the British Isles. In England it favours wet marshy meadows and dry banks of chalk hills. Its principal food is *Scabiosa succisa*, and it is parasitized in its earlier stages by *Apanteles bignelli* and *A. spurius*. A full account of its biology is provided, and its membership of a cline extending across Europe is discussed.

Hunt, J. M. Chalmers- (1952). The history and status of *Pararge aegeria* (Lep. Satyridae) in Kent. *Entomologist*, **85**, 145–154.

A historical review, based on published and unpublished records, of the distribution in Kent and a summary of its present status there. The decrease in the early part of the century may be due to climatic conditions, but there is evidence that the habitat requirements are becoming less restricted, and this may be a major factor influencing the present extension.

Hynes, H. B. N. (1951). Distribution of British freshwater Amphipoda. *Nature, Lond.* **167**, 152–153.

New records of *Eucrangonyx gracilis*, *Gammarus pulex*, *G. lacustris*, *G. tigrinus* and *G. duebeni*.

Hynes, H. B. N. (1952). The Plecoptera of the Isle of Man. *Proc. R. Ent. Soc. Lond.* (A) **27**, 71–76.

Records the stone-flies obtained from sixty-six sites in the Isle of Man.

Ingram, G. C. S. & Salmon, H. Morrey (1952). Ornithological Notes 1948–50. *Trans. Cardiff Nat. Soc.* **80**, 28–33.

Notes on sixty-eight species in Glamorgan and twenty-eight species in Monmouthshire.

Ingram, G. C. S. & Salmon, H. M. (1950). Ornithological notes: 1947–48. *Trans. Cardiff Nat. Soc.* **79**, 45–48.

Notes on unusual or interesting occurrences of fifty-three species observed in Glamorgan and twenty-five species observed in Monmouthshire.

Johnson, C. G. (1950). The dispersal of insects by wind. *New Biol.* **9**, 76–89.

A general account of the subject, with particular reference to recent studies of aphids at Rothamsted; includes a list of references.

Jones, C. Burdon- (1950). Records of British Enteropneusta. *Nature, Lond.* **165**, 636–637.

Saccoglossus serpentinus has recently been obtained from the shores of Mull, whilst *S. cambrensis* has been found at a number of sites on the Welsh coast.

Kimmins, D. E. (1952). *Agrypnetes crassicornis* McLachlan (fam. Phryganeidae), a caddis fly new to Britain. *Ann. Mag. Nat. Hist.* (12) **5**, 1039–1043.

From Malham Tarn, Yorkshire. A key to the British genera of Phryganeidae is given.

Kitching, J. A. (1950). Distribution of the littoral barnacle *Chthamalus stellatus* around the British Isles. *Nature, Lond.* **165**, 820.

Chthamalus stellatus is found west of a line from Dunnet Head to Swanage. Its distribution is discussed in relation to climate.

Le Quesne, W. J. (1952). *Zygina* (*Erythroneura*) *rubrovittata* Leth. (Hem., Cicadellidae) new to Britain. *Ent. Mon. Mag.* **88**, 18.

Leston, D. (1951). *Aradus cinnamomeus* Panz. (Hem., Aradidiae) a bark-bug new to Britain. *Ent. Mon. Mag.* **87**, 285–286. *Aradus cinnamomeus* Panz. (Hem., Aradidae) in Surrey. *T.c.*: 286. *Aradus cinnamomeus* Panzer (Hem., Aradidae) in Berkshire. *T.c.*: 321.

This alleged vector of fungus diseases of young Scots pine was recorded for the first time in Britain, from this food plant at four places in Surrey and one in Berkshire in 1950 and 1951. The first paper contains a key for its separation from other British species of *Aradus* and the second a summary of information on its bionomics in Britain.

Longfield, C. (1952). Notes on the British Odonata for 1950 and 1951. *Entomologist*, **85**, 62–65.

Includes new county and breeding records and deals with some thirty species.

MacDonald, R. (1951). The Crustacea, Amphipoda, of Belfast and Strangford Lochs. *Ann. Mag. Nat. Hist.* (12) **4**, 280–288.

A systematic list, with some details of localities.

MacDonald, R. (1953). The Marine Crustacea, Amphipoda, of the Counties Antrim and Londonderry. *Ann. Mag. Nat. Hist.* (12) **6**, 282–285.

A list with localities.

Mattingly, P. F. (1951). *Culex* (*Culex*) *torrentium* Martini, a mosquito new to Great Britain. *Nature, Lond.* **168**, 172.

This species was taken from water tanks on allotments at Isleworth, Middlesex.

Miller, K. H. & Owen, J. A. (1952). A list of insects from the island of Ulva. *Scot. Nat.* **64**, 31–37.

Lists of Odonata, Hemiptera, Lepidoptera, Coleoptera and Hymenoptera from one of the Inner Hebrides.

Millar, R. H. (1952). The littoral ascidians of Argyll. *Scot. Nat.* **64**, 19–25.

Records of ascidians from five localities in Argyll, with notes on habitat and geographical distribution.

Nurse, M. E. (1951). The Redwing and Fieldfare Enquiry in Wiltshire. *Wiltsh. Archaeol. Nat. Hist. Mag.* **54**, 68–72.

Notes on arrival and departure dates, winter distribution, flock numbers, habitat preferences, feeding habits and roosting.

Parmenter, L. (1951). Notes on the genus *Empis* (Dipt., Empididae) in Britain. *Ent. Mon. Mag.* **87**, 41–44.

Data on the flight periods and food of twenty-eight British species, with localities from the literature for the remaining ten.

Peirson, L. G. (1951). Autumn migration of passerines. *Wiltsh. Archaeol. Nat. Hist. Mag.* **54**, 73–74.

The stream of migrants along the north escarpment of the Berks. and Wilts. downs is not observed in a gap in the downs south of Marlborough.

Rae, B. B. & Wilson, E. (1952). Rare and exotic fishes recorded in Scotland during 1951. *Scot. Nat.* **64**, 102–111.

An unusual number of rare species were recorded off the coast of Scotland in 1951, especially in July and August. It is suggested that rare-fish occurrences may have ecological and climatological as well as purely faunistic significance, and should be correlated with hydrographic data over a number of years.

Reid, D. M. (1951). Northward distribution of *Gammarus pulex* (L.). *Nature, Lond.* **168**, 126.

The northern limit of the freshwater shrimp *Gammarus pulex* in northern Inverness overlaps with the southern limit of *G. lacustris*.

Rice, C. (1952). The redstart in Wiltshire: report of an inquiry conducted during 1949–50–51. *Wiltsh. Archaeol. Nat. Hist. Mag.* **54**, 327–331.

A summary of the status of *Phoenicurus phoenicurus* in those parts of the county where observers were available, with some rather scanty information on habitats and population.

Ruttledge, R. F. (1950). A list of the birds of the Counties of Galway and Mayo showing their status and distribution. *Proc. R. Irish Acad.* **52** (B), 315–381.

Distribution in the counties; status; times of arrival and departure of summer and winter visitors; change in status since 1900 and 1912. There has been an increase in eleven species: Goldfinch, Siskin, Fulmar, Pintail, Shoveler, Tufted Duck, Merganser, Black-tailed Godwit, Sandwich Tern, Black-headed and Common Gulls; and a decrease in eight: Golden and White-tailed Eagles, Yellow Wagtail, Ring Ouzel, Corn Bunting, Stonechat, and Arctic and Common Terns.

Sankey, J. H. P. (1951). Notes on the lateral distribution of some British harvest-spiders (Arachnida, Opiliones). *Ent. Mon. Mag.* **87**, 238–239.

Contains comments on the range of eleven species.

Smith, K. G. V. (1952). Notes on the Macrolepidoptera of Central Shropshire, 1948–51. *Entomologist*, **85**, 25–32.

Contains topographical and geological information, brief descriptions of the localities worked, and a species list giving dates, localities, abundance, food plants and parasites.

Southgate, B. J. & Woodroffe, G. E. (1951). Some observations of Hemiptera-Heteroptera in Buckinghamshire. *Ent. Mon. Mag.* **87**, 103.

Southgate, B. J. & Woodroffe, G. E. (1951). Hemiptera-Heteroptera in Buckinghamshire: an additional note. *Ent. Mon. Mag.* **87**, 201.

Southgate, B. J. & Woodroffe, G. E. (1951). Some recent noteworthy captures of Hemiptera-Heteroptera. *Ent. Mon. Mag.* **87**, 274.

Notes on occurrences, generally with habitats and seasonal data. Includes new records for Middlesex, Berkshire and Wiltshire.

Southward, A. J. (1950). Occurrence of *Chthamalus stellatus* in the Isle of Man. *Nature, Lond.* **165**, 408–409.

The tide-level, density and size of *Chthamalus* at ten stations in the Isle of Man are described.

Southward, A. J. (1951). Distribution of *Chthamalus stellatus* in the Irish Sea. *Nature, Lond.* **167**, 410–411.

The Irish Sea coasts have been surveyed and the distribution of *Chthamalus* is discussed in relation to the position of the shores it occupies, the salinity of the sea-water and the accompanying climate.

Spooner, G. M. (1951). Distribution of British freshwater Amphipoda. *Nature, Lond.* **167**, 530.

Records of *Eucrangonyx gracilis*, *Gammarus pulex*, *G. lacustris*, *G. tigrinus* and *Niphargus* sp.

Stelfox, A. W. (1952). Mollusca at high altitudes in the Scottish Highlands. *J. Conchol.* **23**, 271–272.

Habitats of land and fresh-water snails on Ben Lawers.

Stroyan, H. L. G. (1952). Records of Cambridgeshire Aphididae. *Entomologist*, **85**, 234–236, 249–259.

An incomplete list of some 230 species and subspecies based largely on the author's records, but also on the literature and on preserved material, with dates, localities, food plants and habitats.

Stubbings, H. G. (1950). Earlier records of *Elminius modestus* Darwin in British waters. *Nature, Lond.* **166**, 277–278.

The Australasian barnacle *Elminius modestus*, reported common around Portsmouth and the Isle of Wight.

Tegner, H. S. (1953). The present distribution of the roe deer in Great Britain. *Naturalist*, 19–21.

Gives a brief account of the history of the roe deer in England and Scotland and summarizes the present status.

Vane, F. R. (1950). The birds of Hornsea Mere, Holderness, East Yorkshire, winter, 1949. *Proc. Lpool Nat. Fld Cl.* **1949**, 20–24.

A list of the birds seen on four visits in January and February to a large fresh-water lake only a mile from the sea.

Varley, G. C. (1951). Mosquitoes (Dipt., Culicidae) from Northumberland. *Ent. Mon. Mag.* **97**, 312.

Includes new county records, some of which considerably extend the known distribution of the species concerned.

Walsh, G. B. (1951). New Coleoptera records in Yorkshire. *Ent. Mon. Mag.* **87**, 256–259.

Eighteen new comital and eighty-six new vice-comital records.

Went, A. E. J. (1951). Movements of salmon along the coasts of Northern Ireland. *Nature, Lond.* **167**, 981.

Sites of recapture of sixty-two out of 152 fish tagged in Antrim are cited.

Went, A. E. J. (1951). Movements of salmon around Ireland. I. From Achill, Co. Mayo. (1948 to 1950). *Proc. R. Irish Acad.* (B) **54**, 169–201.

Salmon captured at three centres in Co. Mayo were tagged and released. 95% of the recaptures south of the stations were within 50 miles, while only 35% of the recaptures to the north were within this distance, recaptures from 500 miles to the north being recorded. Apparent rates of travel of up to 33 miles per day were observed.

Wild, A. M. (1952). Additions to the known Spider Fauna of Glamorgan, Carmarthen, Monmouth and other Counties in the British Isles. *Trans. Cardiff Nat. Soc.* **80**, 8–11.

Mainly a record of collecting in South Wales. Seventeen species new to Glamorgan were taken, three of them new to Wales of which one is a new record for the British Isles.

Williams, C. B. (1950). Butterfly migrations. *New Biol.* **9**, 58–75.

A brief account of what is known at present; includes a classified list of migrating British species.

Williams, T. S. (1952). Notes on summering oystercatchers in the Dee estuary. *Proc. Lpool Nat. Fld Cl.* **1951**, 10–12.

Upwards of 500 non-breeding *Haematopus ostralegus* summer on the Flintshire side of the estuary, but very few on the Cheshire side.

Williamson, K. (1952). Migrational drift in Britain in autumn 1951. *Scot. Nat.* **64**, 1–18.

An important paper restating the thesis of Rintoul & Baxter (1918) that the so-called 'rushes' of migratory birds on the east coast of Great Britain are due to drift during periods of easterly or south-easterly weather, and illustrating it from the observed facts of the autumn migration of 1951.

Woodroffe, G. E. (1951). Some further additions to the Buckinghamshire list of Hemiptera-Heteroptera. *Ent. Mon. Mag.* **87**, 236.

6. REPORTS OF ORGANIZATIONS

Fair Isle Bird Observatory (1951). *Second Annual Report*, 1950. 46 pp. (Price to non-members, 2*s.* 6*d.*, Hon. Sec., F.I.B.O., 17 India St., Edinburgh 3.)

Includes detailed notes on migration, trapping and ringing of birds for the 1950 season, also a report by R. Edwards on bird ectoparasites, special studies of certain breeding birds, notes on field taxonomy, and a statistical analysis of wheatear weights.

Fair Isle Bird Observatory (1951). *Bulletins Nos.* 1–5. (Issued to Friends of Fair Isle from 17 India St., Edinburgh 3.)

No. 1 (16 pp.) includes notes on blackbirds' loss in weight in hard weather, geographical variation in the weight of the wren, bird ectoparasites, water-rail weights, and the distribution of age and sex groups in migrant blackbirds.

No. 2 (28 pp.) includes a comparison of the early spring migration at Fair Isle and the Isle of May, and a note on a method of trapping red-backed shrikes.

No. 3 (36 pp.) includes an account of the spring migration at Great Saltee in S.E. Ireland, and in the south of Shetland; notes on a visit to Foula (Shetland), and a note on bird parasites.

No. 4 (32 pp.) contains notes on a study of the breeding colony of arctic skuas on Fair Isle.

No. 5 (48 pp.) contains notes on the autumn migration at Fair Isle, south Shetland, the Isle of May, Noss Head (Caithness), north Sutherland, the Flannan Isles, Little Ross Lighthouse (Galloway), and Great Saltee (Ireland).

Fair Isle Bird Observatory (1952). *Bulletins Nos.* 6–8. (Issued to Friends of Fair Isle from 17 India St., Edinburgh 3.)

No. 6 (48 pp.) includes the Annual Report of the Fair Isle Observatory Trust for 1951, and papers or notes on direct wheatear passage in August 1951, the effects of the gale of January 15, 1952, bird weights, and ectoparasites, all at Fair Isle; also on the autumn migration of 1951 at Portland Bill.

No. 7 (48 pp.) deals with various aspects of the spring migration of 1952 at several Scottish stations and Great Saltee, Co. Wexford, together with a few notes on ectoparasites.

No. 8 (40 pp.) deals mainly with studies of the breeding birds of Fair Isle during 1952, including the Arctic skua, wheatear, black guillemot, fulmar, twite, meadow-pipit and great skua, with some notes on migration at Fair Isle in August, and on the weights of migrant chaffinches.

Farne Islands Committee of the National Trust (1951). *The Farne Islands, Ornithological Report for* 1951. (By G. Watt.) 14 pp.

A disturbing feature of the nesting season was the damage caused by herring- and lesser black-backed gulls, particularly to terns. 106 species were recorded, five for the first time. October was notable for the large number of immigrants and passage-migrants seen at both the beginning and end of the month.

Leicestershire and Rutland Ornithological Society (1951). *The birds of Leicestershire and Rutland: Report for 1950.* (By A. Bonner, R. A. O. Hickling and A. E. Pochin.) (Hon. Sec., R. A. O. Hickling, 66 Hillsborough Rd., Blaby, Leics., 5*s.*)

Includes a census of the great crested grebes (*Podiceps cristatus*) in the counties (196 birds on seventeen waters), and counts of the two races of the golden plover (*Pluvialis apricaria apricaria* and *P. a. altifrons*) on migration at an aerodrome in April.

Lincolnshire Naturalists' Trust (1951). *Bird Observatory and Field Study Centre, Gibraltar Point, Lincolnshire: Report for 1950.* (Price to non-members, 3*s.* 6*d.*, L.N.T., the Museum, Lincoln.)

Work for the year was mainly on migrant and resident birds, but there are notes on Coleoptera, Arachnida and migrant and resident Lepidoptera.

Lincolnshire Naturalists' Trust, Ltd. (1952). *Nature Conservation in Lincolnshire: Third Annual Report, for 1951.* 20 pp. (Hon. Sec., A. E. Smith, 51 West St., Alford, Lincs.)

A list of areas of special scientific interest in the county put forward by the Trust has been approved by the Nature Conservancy and passed to the three county planning committees concerned. The Trust has nature reserves at Gibraltar Point, where there is a bird observatory, and at Decoy Wood, Friskney. It is also surveying important stretches of roadside verge on calcareous soils with a view to ensuring their preservation.

Lincolnshire Naturalists' Trust, Ltd. (1952). *Bird Observatory and Field Research Station, Gibraltar Point, Lincolnshire: Report for 1951.* Compiled by A. E. Smith. 60 pp. (Hon. Sec., A. E. Smith, 51 West St., Alford, Lincs., 2*s.* 6*d.*)

Most of the work at the observatory was on bird migration, but there are notes on bird ectoparasites and other insects, and a useful background physiographical and botanical-ecological survey of the Gibraltar Point area.

Temperley, G. W. (1952). Ornithological report for Northumberland and Durham for 1951. *Naturalist*, 109–129.

Cold weather in April delayed the arrival of the main body of migrants and a continuance of this weather led to a late breeding season. More information is given about migration in the area, while unusual records include Pallas' warbler and American wigeon.

Yorkshire Naturalists' Union (1953). Ornithology division report for 1952. (Ed. R. Chislett.) *Naturalist*, 69–93.

A brief account is given of all birds recorded in the area. Unusual visitors included white-billed divers and a lesser grey shrike. Work at the Spurn Bird Observatory has continued and although fewer birds than usual were ringed the actual number of species marked was a record.

BRITISH ECOLOGICAL SOCIETY

EASTER MEETING IN LONDON

7–8 April 1952

The Easter Meeting of the Society was held in the rooms of the Linnean Society, Burlington House, London. The President, Dr C. B. Williams, took the chair on both these days. The meeting was well attended, about one hundred members being present.

Prof. A. N. Worden and Miss Winifred M. Phillips opened the morning session at 10.30 a.m. with two separate but complementary papers on work they had carried out together with Miss Marie M. Stephens, on the biology of the rabbit in West Wales.

The rabbit has become an agricultural pest of great magnitude in West Wales. For every 100 lb. domestic carcass meat produced in 1946, Pembrokeshire exported 36, Cardigan 24 and Carmathen 10 lb. of rabbit meat, the number of rabbit carcasses railed out of Pembrokeshire approximating two million. From studies involving the recovery of marked individuals, it has been found that commercial trapping operations removes only some 30–40% of rabbits and favours the gradual increase of the population. Foxes and stoats are, however, reduced by rabbit-trapping. There is a high natural mortality during winter, and few rabbits survive into their second year. The intensity of the damage inflicted by rabbits to reseeded pasture has been demonstrated by allowing them to have access to plots approximately 1 acre in extent within a large field. The yield, botanical and chemical composition and lamb-carrying capacity of control plots protected from rabbits remained far superior.

From a study of 7085 rabbits recovered over a 12-month study in north Pembrokeshire it has been found that the highest frequency weight group for both sexes is 1400–1449 g. (live weight) and 1100–1199 g. (paunched weight), but that full-grown males average 32 g. more than females. The main breeding season is January to June, but sporadic breeding occurs throughout the year. The average number of intact embryos was found to rise from 3·39 in January to 5·70 in June. The sex ratio was 100♂ : 100♀ pre-natally, 100♂ : 108♀ up to 6 weeks of age and 100♂ : 136♀ in older rabbits. Coprophagy has been demonstrated at all times of the year and in suckling rabbits.

Cittotaenia species were present in 30·0%, *Cysticercus pisiformis* in 42·1%, *Coenurus cerebralis* in 1·5%, *Eimeria stiedae* in 3·5% and *Fasciola hepatica* in 1·5% of carcasses examined. There was, however, a marked age distribution in the case of *Eimeria stiedae* and a marked geographical distribution in *Fasciola hepatica*.

In the brief discussion that followed, Prof. Varley, Mr Davies and Dr R. E. Hughes took part.

This contribution was followed by a related paper by H. V. Thompson on recent research on rabbit damage. He dealt first with arable crops, in particular spring and winter wheat. In one experiment in Kent in 1950 loss of yield was checked by 3 cwt./acre in spring wheat by fencing.

In the case of pasture an experiment at Wye College, Kent, was described. The number of grazing days and the weight increase of sheep on 3 acres of rabbit-free chalk grassland have been compared with those on a similar area to which a population of rabbits had access. The differences were cumulative over two grazing seasons.

Wire-netting fences are normally used to keep rabbits out of plantations and orchards, but under some circumstances rabbit repellents may be preferred; most efficient protection was given to apple-root stocks by resin (dissolved in ethanol).

In the discussion that followed, Prof. Varley, Mr Davies, Mr Gough and Dr Gorham took part. The significance of these results and those of Prof. Worden and his co-workers was discussed in relation to fluctuation in rabbit population and agricultural production generally.

Dr E. Gorham then gave an account of some factors affecting the development of the humus layer in woodlands. A study of soil properties in some woodland sites in the English Lake District reveals two

very different trends in both surface and profile development, on similar parent material. Under the prevailing high rainfall, topography appears to be the major factor determining whether a flushed brown earth with a *mull* humus layer and ash-sycamore-oak-hazel tree community will develop, or a leached podzolic brown earth with a *mor* humus layer and oak, birch and rowan as the characteristic trees.

In both soil series the capacity of the surface horizons to adsorb cations increases in proportion to the amount of organic matter present. In the *mulls* this increased capacity is largely saturated by bases, in the *mors* by hydrogen ions. As the humus content rises, acidity and base saturation tend to maintain a fairly constant level in the *mulls*, while in the *mors* there is a steady rise in acidity, together with a fall in base saturation.

The discussion that followed stressed the necessity of interpreting the results of some investigations in terms of the comparative physiology of plants. Drs Costain, Watt and Hughes took part in the discussion.

Prof. P. W. Richards opened the afternoon session at 2·15 p.m. with a paper on the ecology of the British species of *Hymenophyllum*. *H. tunbrigense* and *H. wilsoni* have similar, but not identical, ecological requirements. Both grow on rocks and trees in situations where the atmospheric humidity is usually high, but *H. tunbrigense* grows in more sheltered, and frequently in more shady situations than *H. wilsoni*. Thus in the Killarney woods *H. tunbrigense* generally grows on the boulders and the bases of the trees, while *H. wilsoni* is found chiefly on the trunks and branches of the trees and on boulders not in the shade of the wood. In certain Welsh valleys *H. tunbrigense* occurs unmixed with *H. wilsoni* in the lowest parts, while higher up only *H. wilsoni* is found.

Experiments indicate that *H. wilsoni* tolerates more desiccation and is less injured by both high and low temperatures than *H. tunbrigense*, but in order to explain the ecological differences between the two species, both in Britain and in continental Europe, some factor, probably light, in addition to temperature and humidity, must be invoked. Measurements during the winter 1951–2 have indicated that quite large differences of minimum temperature can exist within short distances in a Welsh valley inhabited by both species. Sir Arthur Tansley, Drs Williams, Turrill, Jensen, Hughs, Schelpe, Ovington, Gimingham, Clarke and Ross took part in a discussion, stressing the importance of micro-climatic factors in ecological studies.

Mr R. E. Parker then gave a paper on the Bryophytes of cultivated grassland in North Wales, *Brachythecium rutabulum*, *Eurhynchium praelongum* and *swartzii*, *Rhytidiadelphus squarrosus* and *Acroladium cuspidatum* being studied. They do not produce spores in closely grazed turf and some of them rarely elsewhere. Directly reseeded fields show in their first year *pleurocarp* populations typical of established grassland, while indirectly reseeded fields show only populations of small *acrocarps* characteristic of arable land. These facts suggest the importance of regeneration from gametophyte fragments. He showed that fragments can give rise to new plants after being buried and also on being scattered about the soil surface. Moss populations are characterized by rapid growth during short favourable periods and rapid destruction by drought, grazing, treading and dunging, etc., at other times. The distribution pattern in grassland is subject to seasonal change and largely follows the pattern of animal droppings.

Earthworms not only eat mosses and bury them under casts but they break off shoots and drag them to the mouths of their burrows. Moss fragments can be identified in the faeces of grazing animals showing that they also eat moss although they select against it.

A northern aspect and a moist soil surface free from silting both encourage moss growth; so does over grazing in autumn and winter, especially by sheep. The vigorous leafy swards produced by the better grasses on well fertilized and manured soils are never very mossy. Adequate summer grazing or mowing with lenient rotational grazing at other times further reduces moss growth. The winter treading of cattle while feeding on silage out of doors may also be effective.

Mr Parker was then questioned on several aspects of this work by Dr Schelpe, Sir Arthur Tansley, Drs Gorham, Solomon, Gimingham and Hughes.

Dr C. H. Gimingham terminated the afternoon meeting with a paper on plant ecology on the Aberdeen University expedition to Cyrenaica. This expedition, led by Dr W. B. Fisher of Aberdeen University, visited Cyrenaica for a month in September and October 1951. The expedition was divided into two phases:

(1) Investigation near Derna of the coastal plain and limestone highlands which rise in two successive north-facing escarpments. Behind the purely maritime region (dunes, etc.) to the first escarpment

Poterium spinosum scrub predominates, with characteristic associates increasing in number with increased distance from the sea and altitude. An identical community is widespread in the hills behind the second escarpment at altitudes of 2000 ft. or more, which were worked from the neighbourhood of Cyrene. It forms the first of a series of scrub communities in which structural complexity increases as severity of drought and grazing decrease, each including the components of the previous member of the series together with a superimposed additional structural element:

(*a*) *Poterium* scrub; (*b*) *a*+*Pistacia lentiscus* scrub; (*c*) *a*+*b*+ 'general maquis' with *Arbutus pavarii*, etc.; (*d*) *a*+*b*+*c*+ 'forest'—Olive, *Juniperus phoenicia*, *Cupressus sempervirens*, etc.

(2) Investigation of the ecology of the oasis of Jalo nearly 300 miles south of Benghazi. The extent of the oasis, about 5 miles in diameter, is determined largely by a depression in the desert level, bringing the surface within about 20 ft. of a water-table. The water is saline, containing nearly 0·4% soluble salts, of which NaCl forms a large proportion. Appreciable quantities of salts occur in the surface sand: the habitat is therefore strongly xero-halophytic. The flora of spontaneous perennials consists of only five common species, falling into three structural components: (*a*) woody dwarf-shrubs with succulent foliage, e.g. *Zygophyllum album*, forming low dunes which act as a protective fringe in the north-west sector, the main region of arrival of sand blown by prevailing winds; (*b*) thicket-shrubs—species of *Tamarix*; (*c*) tall trees—tamarisk and date palms. Various crops are grown under primitive irrigation schemes in small cultivated paddocks.

Prof. Osborn, Drs Turrill, Williams and Whitehead took part in the discussion that followed.

At 7.30 in the evening a soirée was held in the Herbarium of the Royal Botanic Gardens, Kew. Two interesting lectures were given by N. L. Bor on 'Vegetation of Assam' and R. D. Meikle on 'Vegetation of Nigeria'.

The following exhibits were set out:

F. Ballard	Photographs of Ceylon's Vegetation
R. A. Blakelock	Distribution of Tree Senecios in East Africa
	Some New Records for the British Flora
A. A. Bullock	Photographs of Central African Vegetation
R. W. G. Dennis	Fungi and Bryophytes
R. B. Drummond	Species Common to the Floras of Tropical Africa and the British Isles
L. L. Foreman	Phenotypic Variation in the Malaysian Flora
J. H. Hemsley	*Romulea columnae* in Britain
J. F. Hope-Simpson	Local environment and Population differences in *Festuca ovina* and *F. rubra*
C. E. Hubbard	*Hordeum agriorithon*, an Ancestor of the Cultivated Barleys
R. W. J. Keay	Wind Dispersal in a Nigerian Forest
H. S. Marshall	Photographs of Peruvian Vegetation
R. Melville	Leaf-characters and the Discrimination of Hybrids
E. Nelmes	A Mauritius Sedge Naturalized in the Isle of Rhum
D. A. Reid	Fungi of a Bedfordshire Sandpit
S. Ross-Craig	Illustrations of British Plants
J. Taylor	pH as a Factor in Moss Distribution

The Society is indebted to Sir Edward Salisbury, Dr Turrill, Mr Summerhayes and to Mr Hubbard for the very pleasant and instructive evening spent at Kew.

The morning of 8 April was devoted to three papers on recent work on ecotypic differentiation and flowering in grasses. The discussion was opened by A. R. Beddoes with an account of the work carried out at the Welsh Plant Breeding Station on seasonal variations in the date of inflorescence emergence in populations of *Lolium perenne* (chiefly); and flowering of fruit trees. In the case of *L. perenne* there was found to be a fairly regular sequence in dates of heading, and the relationship held from year to year, although the actual dates varied according to the season. Mild weather during March and April accentuates variability, while severe conditions, such as occurred in 1947, mask it. The number of days from first flowering of the damson Merryweather to the mean date of emergence for Irish perennial ryegrass in 1943, an early season, was 59, and in 1947 only 18. But the mean is 36 days. For the pear Conference, it is 26 days, and for the apple Bramley, 10 days.

Data on heading are available for Irish perennial ryegrass from 1927 to 1951. During this period the most forward spring was in 1945, mean emergence on 26 April, and the most backward 1947, with the mean falling on 18 May, a difference of 22 days. Therefore, for this strain, at Aberystwyth, a normal season is one when mean emergence falls on or very near 7 May.

L. perenne plants from the Midland fatting pastures come into head 3 or 4 weeks later than Irish. This is because the former have longer photoperiodic, and a higher temperature requirement.

The dates of first flowering of various species have been recorded in the neighbourhood of Aberystwyth during the past 10 years. By the use of the data so obtained, especially those from fruit trees (damsons, plums, pears and apples), a reasonably accurate prediction of the date of flowering and heading in *L. perenne* is possible. Such forecasting can be of use to fruit growers and farmers. For example, it would indicate when operations such as spraying, or the onset of grass-drying, would have to be prepared for.

Mr J. P. Cooper then gave a paper on local climate and flowering in ryegrass. Mr Cooper attempted to relate local and seasonal variations in ear emergence of *L. perenne* to local and seasonal differences in photoperiod and spring temperature within the British Isles. This involved: (i) a study of the timing of ear development under controlled temperature and photoperiod; (ii) the collection of ear-emergence data from clonal transplant material over a wide range of latitude and spring temperature.

Most plants of *L. perenne* only respond to an approximate photoperiod after exposure to low temperature, usually obtained by over-wintering out-of-doors. In the early-flowering S 24 strain of this grass this is attained during January and February in the field. In the late-flowering S 23 a more extended low temperature exposure is required.

Ear initiation in response to day length of 11–12 hr. occurs in the early-flowering strains by late February–early March. In the late-flowering S 23, ear initiation does not occur until early April with a photoperiod requirement of 13–14 hr. Following this the rate of ear development is influenced mainly by spring temperature.

Records of ear emergence from transplant centres show a geographical trend, modified by altitude, from early-flowering in the south-west (Scilly, Cornwall) to late-flowering in the north-east (Craibstone, Shetland). But the relative order of ear emergence of early- and late-flowering strains remains the same.

Mr Cooper concluded that the effects of both locality and season are probably due to variations in spring temperature after the critical day-length has been reached. Response to spring temperature is similar in both early- and late-flowering strains.

Mr Cooper was followed by Mr A. D. Bradshaw who read a paper on local environment and population differences in *Agrostis tenuis*.

In order to investigate the detailed pattern of ecological differentiation in a single species a survey was made of population of *A. tenuis* occupying thirty different habitats, several quite close together, within a radius of 10 miles of Aberystwyth. *Agrostis tenuis* was chosen since it is a normal outbreeding plant occupying a large range of habitats and is easy to cultivate. From each habitat a sample of fifty separate tillers was taken at random and these were grown all together in an experimental garden suitably laid out to control error.

A considerable amount of morphological variation between populations was found. Populations differed significantly whenever the environments of their original habitats differed, even if these habitats were only 50 yards apart. The various different types of environment such as sand dune, cliff top, lowland pasture, lead mine, waste ground, hill grassland have their own related type of plant; while similar types of environment occurring in different regions tend to have the same type of plant. Continuously grading environments have a related grading series of populations.

On genetical grounds this pattern is not entirely unexpected. Several authors have shown that the amount of gene flow, due to transference of pollen, in an unbroken spread of wind-pollinated plants is as low as 5% at distances of 50 yards, and so, providing that the selection is severe enough, populations a short distance apart can become and remain distinct.

Several members of the Society took part in a lively discussion that followed. These included Drs Williams, Turrill, Prof. Varley, Mr Davies, Drs Baker, Watt and Hope-Simpson.

The afternoon session was devoted to two papers on animal ecology. The first was by Dr R. S. Millar on the activity rhythms of the wood-mouse and bank-vole. Small mammals have a short-term feeding rhythm controlled by sensations of hunger; and a 24 hr. cycle of activity which may be either *nocturnal*

or *diel*, according to the animal's reactions to light and temperature. Field investigations in Wytham Woods, Berkshire, confirmed that the wood-mouse (*Apodemus sylvaticus*) is strictly nocturnal; and showed that the bank-vole (*Clethrionomys glareolus*) has a diel rhythm similar to that of *Microtus*, being active during day and night. Both species were studied in the laboratory under controlled conditions of light and temperature. Increasing the length of night from 8 to 12 hr. caused the mice to store food in their nests, and their recorded activity was subsequently reduced to about half that shown during 8 hr. nights. The further increase in length of night to 16 hr. did not affect the amount of activity recorded, but did result in a change from a rhythm with bimodal distribution during the night to one with no definite peaks of activity. The bank-voles showed no appreciable response to the change from an 8 to 12 hr. night; but when the night was lengthened to 16 hr. they also reduced their activity outside the nest in about the same proportion shown by mice, and a previous tendency to show peaks of activity during the night disappeared. Comparison of the ratios of day and night activity of the two species indicated that both had a preference for night-time activity which could not be easily accommodated in an 8 hr. night, with the result that composite histograms for each experiment showed sharp peaks. But when a 16 hr. night was reached, this preference was easily satisfied, and individual variations in time of activity became more apparent.

The meeting was terminated by a paper by H. T. Blank on census methods in partridge population studies. Census work on a partridge population involving peaks of up to 4000 birds over a 4000-acre area in west Hampshire was undertaken primarily as a means of elucidating the factors controlling partridge densities, and secondly to measure the effect of any habitat modification that may be carried out. Three complete censuses are carried out annually. In March, after the coveys have broken up and the birds have paired, the first complete census takes place. The second complete census occurs in September as soon after the peak population period as crop conditions will allow. By careful planning and use of transport and ten to twelve men the 4000 acres are covered in 4 days. On the other estates where the manpower is not available the September census is replaced by an August young/old ratio count which in combination with the March census supplies a useful substitute figure for the September census. After the cessation of shooting a third census is made during December. The September census methods are repeated but the individual driving areas are larger. Supplementary information is provided by detailed nesting records (from which an estimate of the total number of chicks hatched can be made) and by examination of the samples obtained as a result of shooting and netting, and from the August young/old ratio count. For investigating particular aspects of population problems (age-composition, local movement, territories, etc.) over 400 partridges have already been individually marked and the analysis of observations on these birds is providing valuable information. Thus, by use of the above methods, a full and accurate picture of the seasonal rise and fall, and age and sex composition of a partridge population is being built up.

At the close of the meeting the President thanked all the contributors for the very interesting papers presented during the two days of the meeting. He also thanked all at Kew who had made the soirée there so successful.

SUMMER MEETING AT SOUTHAMPTON

21–26 July 1952

The Summer Meeting was held at Highfield Hall, Southampton University, between 21 and 26 July.

On the evening of 21 July a soirée was held at Highfield Hall, at which several exhibits were shown dealing with the ecology of the New Forest and Southampton region. Immediately preceding this, the Principal of the University, Sir Robert Wood, cordially welcomed the Society.

Tuesday, 22 July

The excursion opened with a visit to the Lymington Estuary under the leadership of Mr C. E. Hubbard. A very extensive area of *Spartina townsendii* was examined. This community had in recent years shown some recession and reduction in the vigour of growth of individual plants. Some mortality of tillers and

plants was noted. All this has led to the severe erosion of the hitherto stabilized estuarine silt and mud, which has necessitated extensive dredging of the main channel of the river by British Railways.

Some fungal infection of the *Spartina* has been noted, but this alone was not considered sufficient to account for the marked deterioration of the stand that has occurred. The Society was not able to suggest the cause of this nor a means of checking it.

After lunch the members visited New Park, near Brockenhurst, under the leadership of Dr Hockley. Here an opportunity was had to examine the stream fauna of the area.

A visit was made to the origin of the Lymington River, at the confluence of Ober Water and Highland Water. These are acid streams flowing from considerable areas of bog, and with a pH range of 6·1–7·0. The flow is fairly rapid and the bottom is mainly of gravel, with only short stretches of mud and weed. In eddies of the stream a debris of sticks and leaves accumulates, often forming quite large banks. Here the ammocoete larva of *Lampetra planeri* lives just below water level, consuming the finest particles of debris and micro-organisms. The relationship between larval and spawning sites was demonstrated by Dr Hockley.

During periods of heavy rainfall Ober Water floods the adjacent land, leaving quite large and semi-permanent pools. Mr R. E. Hall demonstrated the situations here, and in the main stream, from which he obtained chironomid larvae in mud samples, and reared the adults for identification. Seventeen species were noted, mainly from the stream edge, and three other species were recorded only from the stagnant water.

The leech, *Hirudo medicinalis*, is also common in this locality, and many species of dragonflies, but these were not in evidence on this occasion.

After tea, White Moor, near Lyndhurst, a typical New Forest Valley Swamp, was visited under the leadership of Miss Jean Dilnot.

At the roadside, near White Moor, a well-developed podsol under *Calluna* heath was inspected, and the party then passed from the drier heath through wetter heath with abundant *Sphagnum compactum* to the swamp in the valley bottom, where peat is developed to a depth of 1 metre masking the Tertiary surface drift of Barton sand, and the dominants are variously *Eleocharis*, *Eriophorum angustifolium*, *Myrica* and *Carex rostrata*, always with a carpet of Sphagna. Alder carr, with marginal *Salix atro-cinerea*, masks the course of poorly developed streams. The carr lacks some of the typical fen species, but nevertheless *Carex paniculata* stools are prominent and the pH is above 6·0, in contrast to readings of 4·15 under *Sphagnum compactum* heath and 5·5 in the swamp. Conductivity measurements support the view that the high basicity of the carr soil is due to a supply of base-rich soligenous water flowing in above a gravel bed, which lies at about 30 in. depth, under the permanently water-logged valley bottom peat, whilst acid flushing by water draining in from the surrounding heath influences the marginal communities.

Plants of interest included a patch of *Rhynchospora fusca*, and occasional individuals of *Lycopodium inundatum*. Dr Dahl named about twenty-five species of lichens and Dr Wallace and Mr Austwick found *Inocybe halophila*, which is normally regarded as a sand dune species and was very frequently associated with *Salix repens* in the 'slacks' of Studland, and a species of *Cortinarius* growing together under *Alnus* and *Salix atro-cinerea*.

Members then returned to Southampton.

During the evening Captain C. Diver gave a very interesting account of his work on Studland Heath, this being in the nature of a general introduction to the area which was to be visited the following day (see C. Diver, *Geogr. J.* **81**, 1933, and R. Good, *J. Ecol.* **23**, 1935).

Wednesday, 23 July

First, the party travelled by coach to Hartland Moor, a small bog to the west of Studland, and one of the few sites in the district where deep peat occurs. This area was drastically burnt with flame-throwers after the war but is now being recolonized. The bog surface was composed of Sphagna and associated plants, with non-tussocky *Schoenus nigricans*. A small adjoining valley contained a fen dominated by large tussocks of *S. nigricans*. A fine stand of *Erica ciliaris* was noted on the adjoining heath.

Lunch was taken at Studland Heath after a brief halt at a point from which a bird's-eye view of the whole area could be obtained.

In the afternoon the party split into several groups. Some studied the south end of Little Sea and the

adjoining dunes, while others made their way northwards, completing a circuit of the whole peninsula, which consists of a narrow spit separated from the sea by three rows of dunes with slacks between them and a larger expanse of water, the Little Sea, between the dunes and the land. Stages in the primary succession from strand vegetation to dunes dominated by *Ammophila arenaria* and then dry heath with *Calluna vulgaris* and *Erica cinerea* were seen. In the slacks areas dominated by such plants as *E. tetralix*, *Myrica gale* and *Salix* sp. (resulting from the accumulation of fresh water) were visited. It was noted that the swamp dominated by *Phragmites communis*, *Scirpus* spp., etc., had in places encroached considerably on the Little Sea since the survey was made by Prof. Good (*J. Ecol.* **23**, 1935, pp. 361–405), and that much of the woodland described by him had been felled.

The party reunited for tea and the return journey during which a halt was made to observe the vigorous and healthy *Spartina townsendii* at Holes Bay, Poole Harbour.

After dinner at Highfield Hall, Dr G. Dahl, of Oslo University, spoke on 'The Ecology and Analysis of Scandinavian Mountain Vegetation'. He dealt in particular with high altitude vegetation in Norway, and the part played by such factors as relative duration of snow cover, and the effect of frost pockets. Dr Dahl showed how these factors had such a dominating effect on vegetation that the composition of the plant communities studied was a direct reflexion of the intensity of these factors, and they apparently did not change in nature from year to year. Hence there was little evidence of the kind of succession that we are familiar with in Britain. He went on to suggest that apparent instances of succession between communities here should be re-examined in the light of his observations.

Dr Dahl also demonstrated a continuous temperature recorder which he had devised, and used in the course of his work.

Several members of the Society took part in the discussion which followed. The necessity for detailed ecological work of the kind outlined by Dr Dahl was stressed.

Finally, Dr C. B. Williams thanked the speaker for his paper, and expressed the pleasure of the Society at his presence throughout the Summer Meeting.

Thursday, 24 July

In the morning a stretch of Highland Water south of the main road bridge (Lyndhurst-Wilverley Post road) was visited under the leadership of Dr A. R. Hockley.

This stream is among large beech trees and scattered holly, and has a 2–3 ft. weir under the bridge. Nearly 300 yards of this stream was surveyed by Southampton students in September 1947, and later changes have been recorded. In March/April each year the spawning sites of *Lampetra planeri* have been observed, and the distribution of the larvae. The locations of these sites and factors influencing their choice were described and discussed by Dr Hockley.

Following this, Mr D. R. Browning, the Assistant County Agricultural Officer, demonstrated to the party the scheme, started in 1944, for reclaiming areas of the New Forest for agricultural purposes (World Crops **4** (1), January 1952). The areas visited were between Brockenhurst and Burley. Since the open forest is all common land, permission to enclose up to 1000 acres was granted for a limited period only. The plots selected, usually bearing bracken and gorse, were fenced off and ploughed. Up to 10 tons per acre of chalk were added, as well as some superphosphate and other fertilizers. Arable crops grown first included potatoes and oats, with some wheat and sugar beet. After 3 or 4 years under arable crops, the plots were sown with various grass-clover mixtures, the surrounding fences being removed a year or so afterwards.

The persistence of these leys under very heavy grazing was quite remarkable, though invasion by bracken and gorse was occurring locally.

After lunch at Burley, the party visited Cranesmoor under the leadership of Mr P. J. Newbould. This is a slightly atypical New Forest valley bog. After crossing the marginal heath communities and the wet heath characterized by *Erica tetralix*, *Calluna* and *Sphagnum compactum*, the party were able to contrast the heavily flushed areas bearing *S. papillosum* and *Rhyncospora alba*. Cranesmoor differs from White Moor, visited on the 22nd, in that it has a more extensive *Sphagnum* carpet, no appreciable carr formation, and occupies a fairly large (lake) basin rather than a small river valley. It is remarkable in having nearly 5 m. depth of *Sphagnum* peat in one part.

After tea the party was met at Stoney Cross by Mr P. L. Winchester of the Forestry Commission, under whose guidance a visit was made to Salisbury Trench Enclosure where *Quercus petraea*, which was perhaps the indigenous New Forest oak, was seen to be regenerating abundantly.

Friday, 25 July

For the final excursion on 25 July, lead by Dr J. F. Hope-Simpson, the objective was Butser Hill, near Petersfield—the westernmost hill of the South Downs and also the highest, bearing chalk grassland, scrub and yew woods and a broad plateau of strongly acid clay-with-flints (surface pH 3·9). Although presenting no great floristic excitement, and sadly impoverished by the recent destruction of its plateau grass-heath, Butser Hill is rich in ecological demonstrations which are the more instructive because for over 30 years it has been the scene of published observations by members of the Society—Tansley, Adamson, Watt, and Hope-Simpson.* The party was conducted by Dr Hope-Simpson to the precise viewpoints of photographs taken in 1920 and 1940. With their aid it was seen that one of the yew societies, freed from heavy rabbit pressure, had recently been re-developing in the coombe-head, while another had remained almost stable. By a similar photographic comparison the deep, rabbit-ridden western coombe (Rake Bottom) showed an apparent waxing and waning of its elder scrub. The spur beyond (Ramsdean Down) showed two or three grassland ecotones (e.g. the limit of co-dominant *Poterium sanguisorba*). On its crest, small islands of clay-with-flints were found to bear a sharply localized dominance by *Agrostis* (*canina* and *tenuis*). Members who faced a whirlwind battle-course across Rake Bottom saw *Rhacomitrium lanuginosum*, a moss otherwise almost unknown on the chalk, and a little *Phyteuma tenerum*, a straggler from its region of great abundance centred a good 30 miles to the east. Tea was followed by a short inspection of the nearby Windmill Hill, where a further photographic comparison showed that the rabbit-devastated ground of 1940 now, after war-time destruction of rabbits, bore an almost closed fescue turf. *Sonchus* sp. was seen by a shaded trunk reaching a height of 6–7 ft.

This terminated a very successful Summer Meeting, during which so much of ecological interest was seen. The weather was excellent, and everyone thoroughly enjoyed the beautiful countryside through which we passed.

The Society is greatly indebted to both Miss F. M. London and Dr Manners who were respectively responsible for the arrangements and for accommodation, travel and food during the itineraries, and for leading many of the excursions.

We also thank Sir Robert Wood, and Prof. W. T. Williams for the hospitality given us at Highfield Hall, and Dr Hockley and Dr Hall for leading the fresh-water biology excursions.

AUTUMN MEETING AT LIVERPOOL

17–19 September 1952

The Autumn Meeting was held at the Department of Zoology, The University, Liverpool, by kind permission of Prof. Pumphrey, F.R.S. Local arrangements were made by Dr H. B. N. Hynes. Members and visitors attending (30) were accommodated at Derby Hall.

On the evening of 17 September at 8 p.m. a Soirée was held at the Department of Zoology, at which Dr J. W. Jones exhibited his film of spawning salmon.

18 September was devoted to a symposium of stream fauna. Dr C. B. Williams was in the chair.

The first paper was given by Dr L. Davies on quantitative studies on the black-fly *Simulium ornatum* in a lowland stream. The work was carried out on, and near, a small stream in east County Durham, where *S. ornatum* composed about 99% of the Simuliid aquatic stages. Fortnightly samples of larvae and pupae were taken at three stations. Up to September of the first season's work, the figures indicated three peaks of pupal abundance, producing adults in April, late May and June, and in August, respectively.

Oviposition activity was studied by means of cylindrical sticky-traps placed horizontally a few inches above water-level, at suitable sites. Three such traps caught up to 300 female *S. ornatum* per week. Great

* Tansley & Adamson, *J. Ecol.* **13**, 1925; A. S. Watt, *J. Ecol.* **14**, 1926; J. F. Hope-Simpson, *J. Ecol.* **28**, 1940; **29**, 1941.

fluctuations in the weekly catch appeared to be mainly due to variation in the attractiveness of the oviposition-sites in the immediate vicinity of each trap. Observations were made on some of the factors governing the attractiveness of sites to gravid females. These factors included the water velocity, presence or absence of vegetation trailing in the water and the amount of splashing of the water.

Removal of the sticky-trap catches at hourly intervals on certain days showed that all but a few *S. ornatum* females laid their eggs during the hour following sunset, although on dull days in September, much oviposition activity was observed about 2 hr. before sunset.

All females caught on such traps were gravid and were accompanied by a negligible number of males.

Studies of biting activity on cattle within half a mile of the stream showed that in calm weather biting commenced less than an hour after dawn and continued throughout the day until dusk, with a large peak of biting activity about 1–2 hr. before dusk.

In the discussion which followed the President suggested that suction traps might be used to catch adult *Simulium*, and, when Dr Davies remarked that electricity was not usually available in the places where this sort of work was done, said that he had known of a small water wheel used to generate current for this purpose. In a discussion of larval density Prof. Varley pointed out that, in species with a restricted oviposition site, the gradual spread of the larvae after hatching made catches of small and large larvae per unit area difficult to compare. Further information suggested that the biting of *Simulium* is not much affected by temperature, is reduced by wind, and controlled mainly by light intensity.

Miss R. M. Badcock then gave a paper on comparative studies in the population of streams. In her initial remarks Miss Badcock dealt with the problem of classifying streams for comparative purposes. In view of their great environmental complexity comparative quantitative data on the fauna of different streams had to be treated with caution. Nevertheless, where methods and seasons are comparable, certain conclusions can be drawn from a study of the numbers of organisms in quantitative samples, a point which may be illustrated by reference to samples from tributaries of the Welsh Dee and of the Kävlinge River system in southern Sweden. These samples of fauna from stony stream-beds indicated a denser population at the Swedish stations than at the Welsh and a decrease in the fauna in winter samples from stones in all stations. Quantitative sampling also helped in assessing predominant organisms and depicting the stream community.

Various factors thought to be involved in differential qualitative and quantitative distribution were discussed with reference to these Swedish and Welsh streams. Important factors in this survey were considered to be:

(1) Geographical location.

(2) A wider temperature range in the water at the Swedish stations (0–24° C.) than at the Welsh (1–16° C.).

(3) A lower rainfall in the Swedish area than in the Welsh, which together with more wooded land in the upper reaches of the Swedish streams, reduced the tendency to scouring spates at the Swedish stations, resulted in lower normal water velocities and permitted the occurrence of more sheltered micro-habitats.

(4) Chemical composition of the water. The water at the Swedish stations was more alkaline and harder than at the Welsh. Calcium content of the water—or perhaps the balance of salts—may have some direct chemo-physiological effect on certain organisms but it seems more likely that in the majority of cases water—or more eutrophic water—influences the fauna indirectly by increasing the algal food supply. The water was well oxygenated at the sampling stations and oxygen was not considered to be a differential factor in this survey.

(5) Shelter provided by vegetation. *Cladophora* at the Swedish stations may have increased the population density of certain organisms, e.g. *Ephemerella*, amongst stones by providing local concentrations from which they could radiate to the bare stones.

As the streams were well stocked with fish at all the sampling stations it is unlikely that the denser invertebrate population in these Swedish streams is connected with relative paucity of fish predators.

A discussion followed on sampling methods, and Dr Macan observed that Miss Badcock's technique probably missed many nymphs of *Rithrogena* (Ephemeroptera) as these cling tightly to small stones. Prof. Varley thought that the lumping together of all species in one order was not justified, and that distinction between carnivores and herbivores should be made. E. D. LeCren pointed out that figures based on surveys of the type described represented standing crops and that two rivers with similar

standing crops at any given time might differ markedly in productivity. He thought that the rate of digestion of food by fish required further study.

Dr H. B. N. Hynes then gave an account of *Gammarus duebeni* in fresh water. The normal habitat of *G. duebeni* is brackish water in which it occurs from Siberia to France and all round the British Isles. In some western British Isles it is reported from purely fresh-water habitats.

Reliable records of the occurrence of this species and of *G. pulex* in Britain have been collected and mapped and these show that the distribution of the two species are quite vicarious. *G. pulex* occupies most of the British mainland, while *G. duebeni* occupies the islands, e.g. Shetland, Fair Isle, Orkney, Inner and Outer Hebrides, Ireland, Isle of Man, Holy Island, Bardsey and Stockholm. *G. pulex* is known only from a few islands.

In two areas, however, both species occur on the same land mass. These have been investigated in detail and are The Lizard and the Isle of Man. In the former it is clear that *G. pulex* is at its westerly limits and has only relatively recently got to the peninsula. It is suggested that in time it will push *G. duebeni* out of the streams it now occupies, from which *G. pulex* is still absent. In the Isle of Man, it seems clear that *G. pulex* is a recent introduction. Here the two species actually occur together in two watersheds, but it can be shown that conditions in both tend to prevent their mixing.

It is concluded therefore that *G. pulex* can replace *G. duedeni* in fresh water. The same appears to apply to marine species of *Gammarus* in the sea itself.

Work is continuing with introduction experiments in the Isle of Man, but this has so far proved inconclusive, and seems to take a long time to bear fruit.

Work has also been done on the suggestion that fresh water and brackish water specimens of *G. duebeni* belong to different biological races, but the conclusion is that they do not. The distribution of the fresh-water type is, for instance, very scattered, they cannot be shown to differ in salinity tolerance or structure of the antennal gland, and they interbreed readily and produce normal offspring.

Several points require further elucidation, the most important being the unexplained absence of both species from apparently suitable streams. This does not appear to be due to water chemistry nor associated organisms.

During the ensuing discussion Dr Hynes said that there was no apparent connexion between the absence of *Gammarus* from certain streams and the presence of any other animal; and that although *G. duebeni* has been kept successfully in the laboratory in the Isle of Man in water from the stream whence it was taken, this has not been achieved in Liverpool. Prof. Varley applauded Dr Hynes's transplantation experiments and said he thought the apologetic references to them quite unwarranted.

Dr Janet Harker followed with her paper on the migration of a mayfly nymph. Quantitative studies of the nymphal population of *Ecdyonurus torrentis* in a Lancashire stream showed that there was a sudden drop in numbers downstream in November, 1949, 1950 and 1951, coinciding with an increase in numbers upstream. Marked nymphs released and collected again after 24 hr. were found to have moved some distance upstream. Laboratory experiments show that there is a marked increase in activity at this time. A similar increase in activity can be affected by lowering the temperature of the water and placing the nymphs on an unstable bottom; these two conditions being also apparent in the stream on the occasions when migration occurred.

Studies of the diurnal rhythm of the nymphs show that the greatest activity occurs between 5·0 and 7·0 a.m., and probably most of the migration takes place in this period. Marking experiments carried out only between 9·0 a.m. and 5.0 p.m. showed that there had been no appreciable movement during those hours.

An increase in numbers downstream in February was noted, but was not as great as the upstream increase in November. Marked nymphs were found to move very slowly downstream at this time, and the activity was not increased. These results suggest that the nymphs tend to be washed downstream as the ice cover breaks, and that no true migration occurs in early spring. In reply to questions Dr Harker said that the upstream migration that she had observed did not lead apparently to crowding near the top of the stream, and that she had not observed a downstream migration at any time of year.

T. T. Macan opened the afternoon session by giving a paper on *Ephemeroptera* of a stony beck. The stream studied was small, being 1000 yards long, and receiving not far from the source two tributaries which rise rather further from the mouth than this. The width probably nowhere exceeds 2 yards and the

water comes up to the ankles during normal flow. The level rises rapidly when there is heavy rain. The flow has not been measured; the significant point is that the current is of such speed that the bottom is stony. The fall is about 100 ft. per mile in the last two-thirds and thrice that in the upper third. There is little vegetation. The beck drains agricultural land.

Ephemeroptera nymphs have been collected from six stations every month for 3 years. The collections have been made with a net; a fine net catches an astonishingly large number of tiny nymphs that pass through coarser netting. A shovel sampler bringing up a known area of bottom which is then tipped into calcium chloride solution so that the animals float to the top has been used.

The common species are *Baëtis rhodani* and *Rithrogena semicolorata*; also abundant are *Ecdyonurus torrentis*, *Baëtis pumilus* and *Ephemerella ignita; Ecydonurus venosus*, *Heptagenia lateralis*, *Habrophlebia fusca*, and *Paraleptophlebia submarginata* occur regularly though in small numbers. The composition of the population has been unexpectedly constant during the three years.

Rithrogena is a univoltive species that emerges in May and lies dormant in the egg stage during the summer. *Ephemerella ignita*, on the other hand, lies dormant in the egg stage all winter and nymphs are found only in summer. Both species of *Baëtis* have several generations in a year.

B. rhodani goes downstream just before emergence and some of the other species probably do the same.

Ecdyonurus torrentis in the lowest reaches of the stream and *Rithrogena* higher up are possibly vicarious to some extent, and *Ephemerella ignita* has been found only in the lower reaches. Otherwise the composition of the population is similar all up the beck, though total numbers are much smaller in the tributaries.

The President and Prof. Varley both thought that Dr Macan was wrong in believing that big annual fluctuations in the populations of species were usual.

An account was then given of spates as a factor in the ecology of rivers by Mr W. R. Munro. There are three main ways in which spates may affect the fauna of a river. First, where the bottom is unstable, many organisms may be crushed and destroyed by the molar action of moving stones. Secondly, they have an indirect effect upon the fauna through alterations in the food supply and in the arrangement of bottom materials. Thirdly, even in rivers with stable beds, it has been suggested that spates bring about a redistribution of the fauna, reducing the population in the more exposed parts of a river and depositing the animals so dislodged in the quieter and more sheltered habitats, from which the depopulated areas are reinvaded during normal water conditions.

Work carried out on the upper reaches of the River South Esk in Glen Clova, Angus, although limited in its scope, appeared to confirm the last-mentioned effect of spates, with particular reference to the Plecoptera and Ephemeroptera.

The results also indicated that there were differences in the average size of nymphs of some species of Plecoptera in two different habitats. It is possible that such differences are due to the selective manner in which spates may affect different size groups of the same species and that the nature of the substratum may be important in this respect. Dr Macan thought that the sampling method used was also open to the objection that many Rithrogena nymphs would be missed. He also asked if Mr Munro could tell the meeting anything about the trays which had been used for sampling at Pitlochry. Mr Munro replied that he had not had any experience of this work but believed that the technique had not proved very satisfactory. The President stressed the necessity of having some indication of the magnitude of error involved in any set of samples.

The final paper of the symposium was given by A. Swain on the fauna of the Nene and Welland. Both the Nene and Welland are strongly influenced by the Lias Clay lands which they drain. They have cut through relatively soft sediments giving rise to silted conditions which favour a preponderance of slow-water communities, particularly on the Nene.

The fauna may conveniently be grouped into 'marginal' forms and 'bottom' forms. The marginal forms inhabit the fringing vegetation and contain, for example, the larvae of Ephemeroptera, Odonata, Trichoptera, and Plecoptera, and also Corixids, fresh-water shrimp and snails. The bottom form consists mainly of Chironomid larvae and Oligochaet worms.

In general, the fauna of the River Nene is varied, except where conditions due to artificial causes occur. For instance, below Earls Barton where a large amount of organic material enters the river, there is a well-defined decline in the fauna, both in species and numbers, except for bottom forms. Further

downstream the marginal forms decrease while the bottom forms remain numerous, and eventually, near Islip, the bottom forms decrease to low numbers. Below this point, there is a gradual increase in the numbers and species of animals.

The character of the River Welland is rather different from that of the Nene. At many places the river is shallow and swift flowing, with the bottom consisting of stones and rocks. Much of the vegetation grows on these stones and harbours a rich fauna which is more or less equally distributed throughout the whole width of the river.

In comparing the Nene with the Welland it is apparent that the fauna of the two rivers owes much to the configuration of the two channels. In the case of the Nene there is usually a shelf extending a few feet from either bank, on which most of the aquatic vegetation grows, and the rest of the channel is deep with a muddy bottom. The Welland, however, is a shallow river along a greater part of its length with little distinction between marginal and bottom fauna. Mr Swain was asked about species identification and he replied that for most groups this had not been done.

The President, in his final remarks, thanked Prof. Pumphrey for his hospitality and the facilities put at the disposal of the Society, and also Drs Hynes and Jones for the excellent arrangements made for the meeting.

Excursion on 19 *September*

A party of some twenty people proceeded by bus to Bala, stopping on the way to look at a small stream and also to visit the experimenta tank on the River Alyn where Dr J. W. Jones's work had been done. After lunch in the town the party went to Bala Lake and spent about an hour there, some people going out on the Liverpool University Zoology Department launch. The return was by the Dee Valley and, as the rain of the morning had cleared and the sun was shining, the drive was most enjoyable. A halt was made at Llangollen and Dr Hynes showed members *Eucrangonyx gracilis*, the American amphipod that has recently reached Britain and which is still confined to a very short stretch of the River Dee.

BRITISH BRYOLOGICAL SOCIETY MEETING AT LEEDS

26–28 September 1952

The British Bryological Society extended an invitation to members of the Ecological Society to take part in their autumn meeting. Several members of the Society took advantage of the invitation to attend as guests, and all appreciated the opportunity to join in a meeting which was very successful and enjoyable.

The meeting, attended by about fifty people, began with a soirée in the Botany Department, University of Leeds, on the evening of 26 September, at which a variety of exhibits of Bryological interest were on view. The following day four papers were read:

Morning

Dr C. H. Gimingham and Miss E. M. Burnett — Investigations of correlation between growth-form and habitat in mosses.

Prof. A. R. Gemmell — Regeneration in *Atrichum undulatum*.

Afternoon

Dr P. Greig-Smith — Taxonomy of British species of *Lejeunea*.

Prof. I. Manton — The spermatozoid of *Sphagnum* and other Bryophytes.

Each of these papers was followed by a lively discussion, and in connexion with the last one Prof. Manton had on view a large selection of remarkable electron microscope photographs showing the spermatozoids of *Sphagnum* and other Cryptogams, in which details of the structure of cilia were demonstrated.

On 28 September an excursion to the woods and riverside near Bolton Abbey, Wharfedale, took place. A large number of interesting species of Bryophytes and Lichens were collected. The enjoyment of a very profitable day was enhanced by the beautiful autumn coloration of the Bolton Woods.

Members were accommodated in Lyddon Hall, University of Leeds. Their gratitude is expressed to Miss L. I. Scott, President of the British Bryological Society, for arranging a programme of general interest, and to Prof. Manton for the hospitality of her Department.

THE ANNUAL GENERAL MEETING

Tuesday, 6 January 1953

The Annual General Meeting was held in the Department of Botany, University College, Gower Street, London on 6 January 1953, by kind invitation of Prof. W. H. Pearsall, F.R.S., members being accommodated at Bentham Hall. On the evening of 5 January, members were entertained at a soirée in the Department of Botany. Several exhibits were displayed, mainly by members of Prof. Pearsall's staff and his research workers. The demonstration included:

E. Gorham and C. C. Dadd	Chemical aspects of humus type under natural conditions
F. H. Perring	Card index system suitable for ecological investigations
J. Fisher	Bird migration
Dr Pennington	Ecology of the English lakes
Miss J. Laptain	Ecology of Beinn Eiche
Miss Francis Barton	Illustrations of Arizona desert plants
Miss J. Dilnot	White Moor in the New Forest
Mr P. J. Newbould	Crane's Moor in the New Forest
Mr B. Hopkins	Statistical methods in the study of plant distribution

Mr J. Chear showed an interesting and instructive colour film of the Summer Meeting at Southampton.

The Annual General Meeting, 6 January, commenced at 10.30 a.m., the President Dr C. B. Williams being in the chair. There were over 100 members present. The minutes of the last Annual General Meeting were read by one of the Honorary Secretaries, Dr R. E. Hughes. These were accepted and signed by the President subject to minor emendations. Immediately following this the annual report of the Honorary Secretaries was read by Dr R. E. Hughes.

Minutes of the Annual General Meeting, 5 *January* 1952

The last Annual General Meeting of the Society was held at Oxford, in the Department of Botany. The President, Dr W. B. Turrill, was in the chair. The meeting was well attended, 120 members being present.

The minutes of the last Annual General Meeting were read and signed. These were followed by the Reports of the Honorary Secretaries and Treasurer. It was reported that the Council of the Society has authorized an increase in the price of both *Journals* to non-members, i.e. *Journal of Ecology* 15*s*. and *Journal of Animal Ecology* 10*s*. per volume. Captain Diver proposed, and Prof. Osborn seconded, that the prices of back numbers of both *Journals* should be increased by an equivalent proportional amount. Prof. Osborne proposed, and Dr A. S. Watt seconded, that such increases in the price of back numbers should also apply to purchases of these volumes made by members. Both proposals were agreed to unanimously. A discussion followed on the financial position of the Society, during which several members criticized certain aspects of the Society's finances. It was agreed that the Treasurer's report to the Society should be made when the auditors' accounts were available, i.e. at a convenient date after March.

The following grants were renewed on the proposal of the President: (i) £10 to the British Freshwater Biological Association; (ii) £5. 5*s*. 0*d*. to the Biological Council; and (iii) £2. 2*s*. 0*d*. to the British Co-ordinating Committee for Nature Conservation.

The auditors, Messrs William Norman and Sons, were re-elected.

Mr Gilson proposed that £20 should be paid to Dr Hobby for assistance in editing the *Journal of Animal Ecology*. This was approved.

The election of Officers and Members of Council followed. These being:

President; C. B. Williams.
Vice-Presidents; C. S. Elton (1 year), W. B. Turrill.
Hon. Secretaries; G. C. Varley, R. E. Hughes.
Hon. Treasurers; V. S. Summerhayes, C. E. Hubbard.
Hon. Editors; H. Godwin, H. C. Gilson.
Hon. Editors of Biological Flora; A. R. Clapham, H. Godwin, P. W. Richards.
Council; H. G. Baker,* A. R. Clapham, D. E. Coombe, C. Diver, C. Gimmingham, J. L. Harley, J. A. Kitching, Miss J. Lambert, E. D. LeCren, A. MacFadyen, E. W. Russell, A. J. Rutter, M. E. Solomon, D. A. Valentine, A. S. Watt*.

In the absence of the new President, Mr C. S. Elton took the chair.

Mr Gilson reported that the first part of Vol. 21 of the Journal of Animal Ecology would appear soon.

Prof. A. R. Clapham noted that there was one contribution during the year to the Biological Flora (N. Woodhead on *Lloydia serotina*). Others would appear during the year.

Following a discussion the Chairman formally proposed that Mr Gilson, the editor of the *Journal of Animal Ecology*, should be left to decide the best form that the notices of publications on animal ecology in the British Isles should take.

Prof. G. C. Varley then opened the symposium on population problems with a paper on 'Population Dynamics in Insects'. He was followed by the following papers:

A. S. Watt	Competition and the Structure of the Community
E. M. Burrows and S. M. Lodge	Intertidal Plant Populations
D. L. Lack	Population Dynamics in Birds
G. D. H. Bell	Population Studies on Certain Arable Crops
D. H. Chitty	Population Dynamics in Mammals
S. Williams	Changes in Plant Populations of Leys during the Establishment Phase

At the close of a very well attended and stimulating meeting Dr W. B. Turrill expressed the hearty thanks of the Society to our hosts Prof. Osborn and his colleagues, also to Prof. Varley for organizing the Symposium and for arranging accommodation for members at Jesus College.

Report of the Honorary Secretaries

The thirty-eighth Annual General Meeting of the Society was held in the Department of Botany, Oxford, on Saturday 5 January 1952. On the evening of 4 January a soirée was held, a wide range of exhibits being shown illustrating ecological work in progress at Oxford and elsewhere.

After the business meeting on 5 January a symposium was held on population problems. Seven papers were read covering diverse fields of investigation on both plant and animal populations.

The Society is indebted to Prof. Osborn for the excellent arrangements that were made for this meeting, and also for his hospitality.

The Easter Meeting (7–8 April) was held in the rooms of the Linnean Society, the President, Dr C. B. Williams, being in the chair. Eleven scientific papers were read, these being:

7 *April*

A. N. Worden, Winifred Phillips and Marie Stephens	Observations on the Biology of the Rabbit in West Wales
H. V. Thompson	Recent Research on Damage by Rabbits
R. Gorham	Some Factors affecting the Development of the humus layer in Woodlands
P. W. Richards	The Ecology of British Species of Hymenophyllum
R. E. Parker	The Bryophytes of Cultivated Grassland
C. A. Gimingham	Plant Ecology on the Aberdeen University Expedition to Cyrenaica

* New members.

8 *April*

A. R. Beddows	Seasonal Variations in the date of Inflorescence Emergence in Populations of *Lolium perenne* (chiefly) and in the First Flowering of Fruit Trees
A. D. Bradshaw	Local Environment and Population Difference in *Agrostis tenuis*
J. P. Cooper	Local Climate and Flowering in Rye Grass
R. Miller	The Activity Rhythms of the Wood Mouse and Vole
H. T. Blank	Census Methods in Partridge Population Studies

On the evening of 7 April a soirée was held at the Herbarium of the Royal Botanic Gardens, Kew. The Society is grateful to the Director, Sir Edward Salisbury, Dr W. B. Turrill, Mr V. S. Summerhayes and Mr C. E. Hubbard for their hospitality and the very pleasant evening spent at the Herbarium.

The Summer Meeting (21–26 July) was held at Highfield Hall, The University, Southampton, 45 members being present. The meeting opened with a soirée at Highfield Hall on the evening of 21 July. Several exhibits of local ecological interest were shown.

On 22 July the field meetings opened with an expedition to the Lymington estuary, where an expanse of deteriorating *Spartina townsendii* was examined.

Other areas visited were New Park, near Brockenhurst, for fresh-water biology, and Whitemoor, a New Forest valley swamp.

During the evening Captain C. Diver gave an account of his work on the Studland Heath. This was fittingly followed on the 23 July by a day's visit to this area. On 24 July the Society examined Crane's Moor, another New Forest Valley bog, New Forest woodlands and some agricultural reclamation work between Brockenhurst and Burley. During the evening Dr E. Dahl, of Oslo University, spoke on 'Ecology and the Analysis of Scandinavian Mountain Vegetation', which stimulated a lively discussion.

The Chalk grassland, scrub, and yew woods of the Petersfield district, particularly Butser Hill, were visited on 28 July.

The Society wishes to thank Miss F. M. Loader for the excellent arrangements for accommodation made at Highfield Hall and the organizing of transport and meals during our itineraries. Our thanks are also due to Dr Manners who planned and led many of the excursions, and to Prof. W. T. Williams for his hospitality. The meeting was very successful and was enjoyed by all.

The Autumn meeting of the Society was held at the Department of Zoology, The University, Liverpool, by kind permission of Prof. Pumphrey. This was devoted to a group of papers on Stream Fauna. About twenty-nine members and visitors attended. The meeting opened on 17 September with the exhibiting of a film of Spawning Salmon by Dr J. W. Jones. Under the chairmanship of the President the following day was devoted to the following papers:

18 *September*

L. Davies	Quantitative Studies on the Black Fly *Simulium ornatum*, in a Lowland Stream
R. M. Badcock	Comparative Studies in the Population of Streams
H. B. N. Hynes	*Gammarus duebeni* in Fresh Water
J. Harker	The Migrations of the Mayfly Nymph
T. T. Macan	*Ephemeroptera* of a Stony Stream
W. R. Munro	Spates as a Factor in the Ecology of Rivers
A. Swain	The Fauna of the Nene and Welland

The meeting concluded on 19 September with an excursion up the Welsh Dee.

The meeting was successful in that it afforded an opportunity for those working in a specialized field to review the more recent advances in that field. The Society is indebted to Dr Hynes and Dr J. W. Jones for the efficient arrangements made for this meeting.

The British Bryological Society held its autumn meeting at Leeds on 26–28 September. By invitation several members of this Society attended.

During the year two parts of Vol. 40 of the *Journal of Ecology* have appeared. The first part contains 246 pages, twelve papers, two reviews, and two contributions to the Biological Flora (*Elymus arenarius* T. E. T. Bond, two species of the genus *Nasturtium*, H. W. Howard and A. G. Lyon).

Two parts of the *Journal of Animal Ecology* (Vol. 21) have also appeared.

During the year the prices of back volumes of both *Journals* have been increased both to non-members and members, the increases being proportional to the increases in the prices of current numbers which were introduced last year.

Membership of the Society has increased during the year from 727 to 768, i.e. by 41. The actual new membership totals 63 (including 6 Associate Members) while 22 have either ceased membership following resignation, death (5) or have ceased paying their subscription.

The Society regrets to report the death of an emminent member in Prof. F. T. Brooks.

An analysis of membership is as follows:

Total	Receive E. only	Receive A. only	Receive E. and A.	Associates	Hon. Members
768	412	221	124	9	2

Members are located as follows: British Isles, 559; Overseas, 209.

The Honorary Treasurer, Mr V. S. Summerhayes, then gave his report on the financial position of the Society. Mr Summerhayes stated that from a preliminary analysis the financial position of the Society was satisfactory. Sales of journals approximately covered costs, and the sum derived from members subscriptions had now reached £1103. Therefore no immediate increase in subscription was contemplated. It was satisfactory to note that the working expenses of the Society were at the low figure of £173. Increased revenue was reported from sales to subscribers (non-members) at the higher prices introduced recently for current and back numbers of both *Journals*. There are apparently no withdrawals of subscriptions due to this increase in prices.

On the motion of the President the Treasurer's report was accepted by the Society.

The President then proposed the renewal of the following grants: The Freshwater Biological Association £10; The Co-ordinating Committee for Nature Conservation £2. 2*s*. 0*d*.

The Society agreed to this.

Dr H. Godwin then proposed that Messrs William Norman and Sons be again elected as the auditors of the Society. This was agreed to.

The President then received the reports of the Honorary Editors.

(*a*) *Journal of Ecology*

Dr Godwin, the editor, reported that the first part of this year's volume was in the press. He also reported that the Council of the Society had agreed to the appointment of Dr D. E. Coombe as Honorary Assistant Editor to the *Journal of Ecology*. Dr Godwin was glad to let members know that he had received a letter of appreciation from a contributor to the *Journal*.

There was no lack of material for publication. Its standard was satisfactory. Dr Godwin, however, appealed to contributors to keep their papers as brief as possible. He called attention to the coloured plates which had recently appeared in the *Journal*, and stated that the expense of publishing these was not borne by the Society.

Dr Godwin reported that there was one more contribution during the year to the Biological Flora.

(*b*) *Journal of Animal Ecology*

Mr Cary Gilson mentioned the change in format of the *Journal*. Two parts of the *Journal* would, he hoped, appear during the year, probably in May and November.

The abstracts of papers on animal ecology did not appear in 1952, but would be resumed in 1953, Prof. L. A. Harvey undertaking to edit them, while R. S. R. Fitter would be responsible for the abstracts of relevant papers from local Natural History Societies. There would be some modification in the grouping of the material.

Both these reports were accepted by the Society.

Mr Gilson proposed that £20 be paid to Dr Hobby for checking the bibliographies in the *Journal of Animal Ecology*. This was agreed to.

The Society then proceeded to the election of officers and members of Council. On the proposal of the President the following were elected:

President; C. B. Williams.
Vice-Presidents; W. B. Turrill (1 year), J. A. Kitching.
Hon. Secretaries; G. C. Varley, R. E. Hughes.
Hon. Treasurers; V. S. Summerhayes, C. E. Hubbard.
Hon. Editors; H. Godwin, H. C. Gilson.
Hon. Editors of Biological Flora; A. R. Clapham, H. Godwin, P. W. Richards.
Council; H. G. Baker, A. R. Clapham, D. E. Coombe, J. B. Cragg, C. Diver, C. Elton, C. H. Gimingham, J. E. Harley, J. A. Kitching, Miss J. Lambert, E. D. LeCren, A. MacFadyen, A. J. Rutter, D. H. Valentine, M. E. Solomon, A. S. Watt.

It was pointed out that as no actual retirements from the Council occurred this year, it was necessary to re-examine the terms of election to it. As certain aspects of the rules were to be examined by the Council during the year it was agreed to consider this also.

Prof. G. C. Varley then brought before the Society some of the proposed changes in the rules of the Society, copies of these being circulated to members during the meeting. There was criticism of the fact that these proposed changes in rules had not been circulated with the programme. Mr Gilson, Mr Chear, Mr Davies and Dr Godwin took part in this discussion. Prof. Varley pointed out that the changes proposed were of a minor nature, removing anomalies, and clarifying them where they were difficult to interpret or conflict with current practice.

The proposed changes were therefore accepted by the Society. The changes in rules were:

For Hon. read Honorary throughout.

Rule 3, line 3, delete the words 'or more other members' and substitute 'other member'.

Rule 4, line 2, delete the word 'minimum'.

Rule 7, line 2, delete words 'not less than'.

Rule 8, after the two existing paragraphs insert the previous rule 17 as para. 3.

Rule 9, line 7, insert the words 'President or' before the word Vice-President.

Rule 13, amend to read 'The two Honorary Treasurers shall be elected for a period of three years and shall be re-eligible. The Honorary Treasurers shall keep the Society's funds and be responsible for the collection of subscriptions. Their sanction shall be required for the disbursement of the Society's moneys. The financial status and policy of the Society shall be considered each year at the meeting of Council held as soon as practicable after the audit. A financial statement shall be made to the Society at its next meeting. The audited accounts shall be published in the Journals of the Society.'

Rule 15, line 1, for 'one fortnight' read 'two weeks'; line 2, for 'members of the Society' read 'Members of the Society resident in the British Isles'.

Renumber rules 18–27 as 17–26.

Rule 19 (now 18) line 2, delete 'later'.

Rule 20 (now 19) line 3, for 'by the secretaries' read 'to the secretaries'.

Rule 21 (now 20) line 1, for 'only be made' read 'be made only'; line 2, for 'Members voting' read 'Members present and voting'.

Notes.

Rule 13. The old rules expect the Treasurers to produce a financial statement at the Annual Meeting. In practice, as the bills for the year have at that time not come in, the only statement possible is very incomplete. The proposed amendment gives the Treasurers the power to present the financial statement when it is complete after audit.

Rule 20 (to be renumbered 19). The proposed change corrects what appears to have been a misprint.

All the other changes are either purely verbal or are clarifications, and remove inconsistencies in the original drafting.

Prof. Varley reported that further changes were likely to be considered by the Council during the year.

At 11 a.m. the President, Dr C. B. Williams, delivered his Presidential address, Dr W. B. Turrill, the Vice-President, taking the chair.

Dr Williams dealt first with the changing outlook in biology in the last hundred years during which, by more insistence on measurement and accuracy, anecdotal natural history has gradually developed into the modern science of ecology.

Most progress in biology is in the form of inferring general laws from a number of special cases (observations) and statistical methods bear the same relation to formal mathematics as inductive to deductive logic. Very few biological laws can be considered as 'true' or 'proved'; they merely become more and more likely to be correct as more and more evidence accumulates that does not contradict them. Uncertainty cannot be eliminated but it can be measured.

One result of the methods of statistical analysis has been the development of the complex experiment instead of the over-simplified type of earlier years. By combining several variables into one field experiment not only the direct results are obtained but also the interactions between the variations and so the results are of wide application. Further, by insistence on replication the significance or reliability of the conclusion can be assessed.

Many biological problems take the form of inferring from a 'sample' what is likely to be true of the 'population'—and it was pointed out that the reliability of the conclusion depends on the total size of the sample, to what extent it can be subdivided, and to what extent it is really randomized—or representative of the whole population. The most difficult to deal with are biased sampling errors in which—possibly for reasons quite beyond the control of the observer—one section of the population is more frequently represented than another in the available sample.

Further samples have certain properties not necessarily found in the population, and in the same way the population often has properties not obvious from the sample—and some quite unlike anything belonging to its component parts.

As an example of the former it was pointed out that if an animal population contained a number of species all equally abundant, they would not be so distributed in the sample.

In discussing measurable qualities of populations it is most important to know not only the total count—and hence the arithmetic mean—of the samples, but to know how the values were distributed in various samples or subsamples. In this connexion the important difference between arithmetic and geometric variations was discussed—and it was shown how in some biological problems the use of arithmetic means can be misleading.

The second half of the address consisted of a rapid survey of some of the ecological problems recently studied from this statistical approach. They included: the quantitative relation between insect activity and weather conditions, the relation between insect populations and previous weather conditions, the relative abundance of species in mixed wild populations, the relative frequency of genera with different numbers of species, inter-generic competition in mixed populations, the distribution of plant species in quadrats, diversity as a measurable ecological character, the number of species in small and large areas, etc.

The afternoon session commenced at 2 p.m. when Dr H. N. Southern gave his paper on 'Balance of Numbers in Owls and small Mammals'.

The work described was an attempt to secure field data on the numerical relations between populations of a predator, the tawny owl, *Strix aluco*, and its two main prey species, the wood-mouse, *Apodemus sylvaticus*, and the bank vole, *Clethrionomys glareolus*. Nobody has yet demonstrated in the field whether a population equilibrium can be maintained between a predator and its prey, but the question is important, both as a general principle of population control and as an economic advantage, if the alternative is the control of the prey by their food. Damage to herbage and crops will obviously be much greater in the latter situation.

The field work was done on a 1000-acre estate, mainly woodland, near Oxford and has lasted 5 years. A preliminary analysis only of the results was presented. The owl population of the whole estate was censused for 6 years and the task was greatly helped by the discovery that these birds are resident and strictly territorial. The number of young produced each year was determined by finding the nests and by counting the fledged young during their long and noisy period of dependence on the parents.

The two species of rodents were censused on 250 acres by the capture-recapture method, which involves the use of live traps and numbered leg rings for marking. From this, estimates were obtained of the total population at times separated by 2-month intervals, and of the numbers of animals entering and leaving the population during each interval. This work was carried on for 4 years and nearly 10,000 animals were marked.

Finally, a monthly collection of owl castings was made to show the proportion of wood-mice and bank voles in the diet from season to season, year to year and territory to territory.

The breeding population of owls remained fairly steady at about twenty pairs throughout the study except in 1947, when the hard winter caused density-independent mortality and only fifteen pairs bred. But breeding success varied greatly from year to year according to the level of the prey populations. Both mortality among fledglings and chilling of eggs (presumably because the males could not bring enough food for the incubating hens) occurred in 1949, 1951 (exceptionally severely) and 1952. Conversely, in 1950, no fledgling mortality was observed and clutches that were lost were replaced.

The population curves for wood-mice and bank voles from 1948 to 1952 show an irregular course. Since the figures for entrants into the population show regular seasonal changes, the irregularities are presumably due to mortality. If the pressure of the predators upon the prey is measured (as a first, rough approximation) by their proportions in the owl castings, an interesting comparison emerges. In autumn 1949 both prey reached a high peak. The owls concentrated on wood-mice, which were heavily reduced. The bank vole was little affected and reached another high peak in the summer and autumn of 1950, whereupon the owls turned to them and reduced them so thoroughly that in 1951 their own breeding season was catastrophically bad (five young were reared compared with a general level of twenty), since the wood-mice still had not recovered from their reduction 2 years earlier. Finally, the smaller autumn population of owls allowed both species of prey to recover in late 1951 and early 1952.

These results suggest tentatively that the availability of prey acts as a density-dependent mortality factor of the predator; furthermore, since changes in the predator population seem to initiate changes in the prey, the control may be mutual.

In the discussion that followed Dr Yapp, Profs. Cragg and Valentine, Mr Chear and Mr Elton took part. It was pointed out that during the 3 years of the duration of life of an owl there was no extension of territory. Differences between the sexes in food preferences were noted. The economic significance of this kind of work was also discussed.

Mr C. D. Pigott then gave his paper on the interpretation of the discontinuous distribution of some members of the British Flora. The discussion was limited to plants which generally occur on soils with a moderate to high base status in unshaded habitats; many of the species are widespread at the present day in eastern, central and southern Europe. The distribution of *Linosyris vulgaris* provides one of the more striking examples. *Linosyris* is widespread in south-east Europe, but towards the northern and western limits of its range it is confined to isolated localities; in Britain to five coastal headlands of Palaeozoic limestone on the west coast. These localities have several features in common; they are outcrops of the hard limestone with shallow pockets of soil and it is probable that these conditions are maintained naturally by the immaturity of the topography and do not depend on human interference for their existence. In the same localities grow many other plants of similar ecological requirements, e.g. *Helianthemum canum*, *H. apennium*, *Hypochoeris maculata*, etc., and the concentration together in these and many similar places, e.g. the Burren, Clare; Upper Teesdale, Durham and Yorkshire; etc., of several relict species is remarkable.

It is tentatively suggested that these distributions are to be related to the historical, rather than the present day, importance of ecological factors. Quaternary research has revealed that, for a long period during and following the retreat of the ice, the broad belt of land between the Alpine and Scandinavian ice sheets was occupied by an open 'steppe-tundra' vegetation in which grasses and species of *Carex*

predominated. Not only were Arctic-Alpine species, e.g. *Dryas octopetala* widespread in the lowlands, but so also were ruderals and many plants now associated with 'steppe' vegetation and calcareous grasslands, e.g. *Helianthemum* spp. The presence in deposits of Late-glacial age of such species as *Potentilla fruticosa*, *Teucrium scordium* and *Polemonium* sp. in areas in which these plants no longer occur, e.g. Nazeing, Essex; Hawk's Tor, Cornwall, suggests that it may well be during the Late-glacial and the early part, i.e. the Boreal, of the Post-glacial that many of these reached their present localities. Subseq uently during the Post-glacial the development of leached soils, peat and the spread of closed forest resulted in their restriction to isolated localities in which these conditions were not prevalent, i.e. cliffs, steep slopes, lake shores, screes, etc.

Progressive forest destruction in the Neolithic period and subsequently has allowed certain of these plants to expand once again, but others, for little understood reasons (low reproductive capacity, low competitive power, biotype poverty, etc.) have been less successful and remain only in the areas in which they persisted through the forest period of the Post-glacial.

Dr S. M. Walters followed, exemplifying the sort of problem which might yield, simply by careful observation, interesting data relevant to the thesis which Mr Pigott had presented.

(1) *Autecological observation*

The case of *Liparis loeselii* (L.) L. C. Rich, the fen orchid, was considered. In Britain its markedly disjunct distribution was in (*a*) East Anglian fens, (*b*) South Wales dune-slacks. Such an ecological disjunction between inland fen and coastal habitats is paralleled by many British species, e.g. *Teucrium scordium* L. and *Samolus valerandi* L. and is susceptible of the general explanation already advanced, viz. that such plants occupied more nearly continuous ranges in the Late-glacial period, and are now present as more isolated select populations, often showing some morphological (sometimes ecotypic) differentiation. Dr Walters presented some evidence that the species had a very low power of competition with the normal fen hydrosere dominants, and indeed had achieved great local abundance in the fens only in disturbed artificial conditions (such as originated after partial drainage and peat-digging). He suggested that precise observation on population variation, seedling establishment, life history, etc., was of obvious importance in understanding this low competitive power, and therefore in suggesting how the fen populations might have survived Post-glacial vicissitudes.

(2) *Distributional observations*

Two 'continental' microspecies of the aggregate *Alchemilla vulgaris* were discussed, viz. *A. acutiloba* Opiz and *A. monticola* Opiz. Both occur in Upper Teesdale; *A. acutiloba* has not been recorded from the British Isles except in that region, whilst three other records only exist for *A. monticola*, all obviously short-lived casuals. The peculiar interest of the relict Teesdale flora (some species of which, e.g. *Viola rupestris*, have general Eurasian distributions remarkably reminiscent of the two Alchemillas) made it of some importance to find out how real was this apparent restriction to Upper Teesdale. Detailed dot distribution maps (prepared by Miss M. E. Bradshaw during 1951 and 1952) for both species in the Upper Teesdale area were shown and discussed. These, though actually incomplete, showed, first, that *A. monticola* was certainly centred in Upper Teesdale, whilst *A. acutiloba* had several centres, the largest being in Weardale a few miles north; and secondly that both showed a pattern of spread which might well be recent and actively in progress, along the main roads out of the valley 'centres'. Dr Walters discussed briefly the possible hypotheses to account for the data, pointing out the importance of having the distributional data before attempting any such discussion. In the discussion that followed Dr W. B. Turrill speculated on the possible relations of limestone and chalk flora, suggesting a migration from the former to the latter. Mr Pigott agreed that this may have occurred to a certain extent. Dr H. Godwin pointed out that this kind of approach was applicable to much of the British flora, but he warned against the over emphasis of the periglacial survival of species. Others who took part in the discussion were Mr Gilbert-Carter, Dr Heslop Harrison, Prof. Valentine and Dr Baker. The importance was stressed of population and experimental taxonomic investigations in the study of relict genera.

At approximately 4.30 p.m. the President concluded the meeting by thanking all who had taken part, and particularly Prof. W. H. Pearsall for his continued hospitality.

LIST OF MEMBERS (30 January 1953)

E. = Takes *The Journal of Ecology*. A. = Takes *The Journal of Animal Ecology*.

Corrections, omissions or changes of address should be notified at once to the *Hon. Secretary*, R. E. Hughes, School of Agriculture, Downing Street, Cambridge

E. **Abdin**, Dr G., M.Sc.; Botany Dept., Faculty of Science, Fouad I University, Abbassieh, Cairo, Egypt.
E. **Abeywickrama**, B.A., B.Sc.; Department of Botany, University of Ceylon, Colombo, Ceylon.
Adams, Miss A. W., B.Sc.; Applegarth, Stocksfield, Northumberland (*Associate Member*).
E. A. **Adams**, Dr Charles C.; 149 Manning Boulevard, Albany 3, N.Y., U.S.A.
E. **Adamson**, Prof. R. S., M.A.; The University, Cape Town, S. Africa.
E. **Adcock**, J. A.; 50 Sandy Lane, Cooper Lane, Norwich, Norfolk.
E. A. **Airey**, A. F., M.B.O.U.; Broadley's Cottage, Ghyll Head, Windermere, Westmorland.
A. **Allee**, Prof. W. C.; 114 Leigh Hall, University of Florida, Gainsville, Florida, U.S.A.
A. **Allen**, E. F., B.A., M.B.O.U.; Dept. of Agriculture, Teluk Anson, Perak, Malaya.
E. **Allison**, Miss I. J., B.A.; 11 High Street, Sandy, Beds.
E. **Allott**, D. J.; 167 Covington Way, Norbury, London, S.W. 16.
E. **Alston**, A. H. G., M.A.; 25 Pelham Crescent, London, S.W. 7.
E. **Anderson**, J. A. R., B.Sc.; Forestry Dept., Sibu, Sarawak.
E. **Andrews**, F. W., D.Sc., Ph.D.; 27 Minterne Avenue, Norwood Green, Southall, Middlesex.
E. **Archibald**, Miss E. E. A., M.Sc.; 42, 13th Avenue, Walmer, Port Elizabeth, S. Africa.
E. **Armitage**, Miss E.; Foxdale, nr Ross, Herefordshire.
Ash, J. S., B.Sc., M.B.O.U.; I.C.I. Game Research Station, Burgate Manor, Fordingbridge, Hants. (*Associate Member*).
E. **Ashby**, Dr Eric; The Queen's University, Belfast.
Ashby, K. R., B.A.; Zoology Dept., The University, South Road, Durham (*Associate Member*).
E. **Ashby**, Dr M.; 2 Redlands, Tiverton, Devon.
E. **Asprey**, Prof. G. F.; The University College of the West Indies, Kingston, Jamaica.
E. A. **Audy**, J. R., M.B., B.Sc.; Institute for Medical Research, Kuala Lumpur, Malaya.
A. **Auerbach**, Dr S. I.; 4450 N. Sawyer Avenue, Chicago 25, Illinois, U.S.A.
E. **Austwick**, P. K. C., B.Sc.; Mount MacGregor, 29 Surrender Crescent, Brighton 6.
E. **Bacon**, Mrs Alice, B.Sc.; 20 Grand Avenue, Hassocks, Sussex.
A. **Badcock**, Miss R. M., M.Sc.; Biological Dept., University College of N. Staffs., Keele, Staffs.
E. A. **Bagenal**, T.; Marine Station, Keppel Pier, Millport, Isle of Cumbrae, Scotland.
E. A. **Baker**, H. G., Ph.D.; Botany Dept., The University, Leeds 2.
E. **Balfour**, Mrs E. J.; Newton Hall, Windygates, Fife.
A. **Balfour-Browne**, W. A. F., M.A., F.R.S.E.; Brocklehirst, Collin, Dumfries, Scotland.
E. **Ballantine**, Miss D., B.Sc.; 'Priors Close', Cambo Place, Cullercoats, Northumberland.
E. **Ballard**, F., B.Sc.; Herbarium, Royal Botanic Gardens, Kew, Surrey.
E. **Bally**, P. R. O.; Botanist, Coryndon Memorial Museum, Nairobi, Kenya, E. Africa.
E. **Balme**, Miss O. E., B.Sc.; Imp. Coll. Field Station, Silwood Park, Sunningdale.
A. **Band**, R. M.; 516 North Drive, Cleveleys, nr Blackpool, Lancs.
A. **Barker**, T. W., B.Sc.; 346 Stones Villas, Walsden, Todmorden, Lancs.
E. **Barkley**, Miss S. Y., B.Sc.; 42 Ovington Square, London, S.W. 3.
E. **Barnes**, B., D.Sc., Ph.D.; 19 High Park Road, Kew Gardens, Richmond, Surrey.
A. **Barnes**, H. F., Ph.D.; Rothamsted Experimental Station, Harpenden, Herts.
E. **Barnes**, Mrs M., M.Sc.; Lorne Villa, The Marine Parade, Millport, Isle of Cumbrae, Scotland.
E. A. **Barrett**, J. H., B.A.; Dale Fort Field Centre, Haverfordwest, Pembrokeshire.
E. **Barry**, D. H., B.Sc.; 7 Tring Avenue, Ealing Common, W. 5.
E. **Barton**, Miss Frances M.; 19 Park Street, Bath.

E. A. **Bates**, Dr Marston; Dept. of Zoology, University of Michigan, Ann Arbor, Michigan, U.S.A.
E. **Baxter**, Miss E. V., F.L.S.; The Grove, Upper Largo, Fife.
E. **Bayer**, Prof. A. W., D.Sc.; Dept. of Botany, Natal University College, Pietermaritzburg, S. Africa.
E. **Beard**, Dr J.; Natal Tanning Extract Co. Ltd., Pietermaritzburg, Natal, S. Africa.
E. **Beddows**, A. R., M.Sc.; Welsh Plant Breeding Station, Penglais, Aberystwyth.
E. **Bell**, Dr G. D. H.; University School of Agriculture, Cambridge.
E. **Bell**, Prof. H. P.; Botanical Laboratory, Dalhousie University, Halifax, Nova Scotia.
E. A. **Bentley**, Dr E. W.; 41 Cumberland Road, Bromley, Kent.
A. **Berg**, Dr Kaj; Köbenhavns Universitets Forskvands, Biologiske Laboratorium, Hillerod, Holland.
A. **Bertram**, Dr G. C. L.; St John's College, Cambridge.
E. A. **Bexon**, Miss D., M.Sc.; University College, Nottingham.
E. **Bhâradwâja**, Prof. Y., M.Sc., Ph.D.; Dept. of Botany, Benares Hindu University, Benares 5, India.
E. **Bharucha**, Dr F. R.; 6 Alexandria Road, New Gamdevi, Bombay 7, India.
E. **Bingley**, F. J., M.A.; Flatford Mill Field Centre, East Bergholt, nr Colchester, Essex.
A. **Birch**, L. C., M.Sc.; Zoology Dept., Columbia University, New York 27, N.Y., U.S.A.
E. **Birmingham Natural History and Philosophical Society**; 114 Oxford Road, Moseley, Birmingham 13 (C. E. A. Andrews, B.Sc., F.L.S., *Hon. Treasurer*).
E. **Birse**, E. L., B.Sc.; Old Schoolhouse, Midmar, Aberdeen.
E. A. **Blackburn**, Miss K. B., D.Sc.; Botanical Dept., King's College, Newcastle-upon-Tyne 2.
E. **Blackman**, Prof. G. E.; Univ. Dept. of Agriculture, Oxford.
E. **Blakelock**, B. A., B.Sc., F.L.S.; The Herbarium, Royal Botanic Gardens, Kew, Surrey.
E. **Blanchard**, Miss B., B.Sc.; Hartley Botanical Laboratories, The University, Liverpool 3.
E. **Blank**, T. H., B.Sc.; 'The Limes', Damerham, nr Fordingbridge, Hants.
A. **Bletchly**, J. D., B.A.; c/o Lloyds Bank, Nailsworth, Glos.
E. **Bloomer**, H. H.; 'Longdown', Sunnydale Road, Swanage, Dorset.
E. **Boatman**, D. J., B.Sc.; 7 Hurst Road, Buckhurst Hill, Essex.
E. **Böcher**, Dr Tyge W.; Universitetets Planteanatomiske Laboratorium, Gothersgade 140, Copenhagen K, Denmark.
E. **Bogdan**, A. V.; P.O. Box 338, Dept. of Agriculture, Nairobi, Kenya Colony.
A. **Booth**, Capt. B. D. McDonald; Royal Scots Greys, M.E.L.F. 5.
E. **Bor**, N. L., C.I.E., M.A., D.Sc., F.L.S.; Royal Botanic Gardens, Kew, Surrey.
E. **Boughey**, Prof. A. S.; University College, Achimota, Accra, Gold Coast.
A. **Bovey**, Prof. P.; Entomologisches Institut der Eidg. Tech. Hochschule, Universitätstrasse 2, Zürich, Switzerland.
E. A. **Bowyer**, F. H., M.B.E.; Barclay Perkins & Co. Ltd., Park Street, Southwark, London, S.E. 1.
A. **Boyd**, A. W., M.C., M.A.; Frandley House, nr Northwich, Cheshire.
E. **Boyko**, Dr H.; Ministry of Agriculture, Ha' kirya, Tel-Aviv, Israel.
E. **Bradshaw**, A. D., B.A.; Dept. of Agricultural Botany, Bangor, N. Wales.
E. **Braid**, Major K. W., M.A., B.Sc.; 'Dunalistair', 48 Buchanan Street, Milngavie, Glasgow.
E. **Braun**, Miss E. L.; Salem Pike, Mt. Washington, R.R. 13, Box 41 C, Cincinnati 30, Ohio, U.S.A.
E. **Braun-Blanquet**, Dr J.; Station de Recherches Géobotaniques, Chemin du Pioch de Boutonnet, Montpellier, France.
E. **Brenchley**, Dr Winifred E., O.B.E.; Rothamsted Experimental Station, Harpenden, Herts.
A. **Brereton**, J. LeG., B.Sc.; 16 Norham Gardens, Oxford.
E. **Brett**, D. W.; 43 Penrhyn Avenue, Walthamstow, London, E. 17.
E. **Brett**, Miss O. E., B.Sc.; 13 The Vale, Woodford Green, Essex.
E. **Brewer**, Prof. H. E.; Department of Botany, State College of Washington, Pullman, Washington, U.S.A.
E. A. **Brian**, M. V., M.A.; Zoology Dept., The University, Glasgow, W. 2.
E. **Brien**, T. R., B.Sc.; St Mary's College, Tregeyb, Llandilo, Carmarthen.
E. **Brierley**, J. K., B.Sc.; 'Greenways', Lilac Avenue, Kingsway, Derby.
E. **Bristol Naturalists' Society**, Botanical Section; c/o Bristol Nat. Library, City Museum, Queens Road, Bristol.

E. A. **Brockhurst**, R. B., M.S.; 1602 Georgia Drive, A-1, Urbana, Ill., U.S.A.
E. A. **Broembsen**, H. H. v., B.Sc.; 134 Verdoorn Street, Sunnyside, Pretoria, South Africa.
A. **Brown**, A. G., M.R.C.S., L.R.C.P.; Colac, Victoria, Australia.
A. **Brown**, E. S., B.A.; Hailey Lodge, Hertford Heath, Hertford.
A. **Brown**, Miss F. M.; 21 Park Square South, Leeds 1.
E. **Brown**, J. M. B., B.Sc.; Forest Research Station, Alice Holt Lodge, Farnham.
A. **Brown**, P. E.; Woodside, Baughurst, Basingstoke, Hants.
A. **Brown**, V. M., B.Sc.; 43 Kensington Gdns, Darlington.
A. **Brownlee**, A., B.Sc.; A.R.C. Field Station, Compton, nr Newbury, Berks.
E. A. **Bullock**, A. A., B.Sc.; Herbarium, Royal Botanic Gardens, Kew, Surrey.
E. A. **Bullock**, W. A. C., B.Sc.; 2, The Pastures, Repton, Derby.
E. **Bulman**, Mrs M.; Wentworth House, Chesterton Lane, Cambridge.
E. A. **Burckhardt**, D.; Im Dreiangel, Sempach, Switzerland.
E. **Burges**, Prof. N. A., M.Sc., Ph.D.; Botany Dept., University of Sydney, N.S.W., Australia.
E. **Burkill**, I. H., M.A.; Clova, The Mount, Leatherhead, Surrey.
E. **Burman**, A. D.; 41 Trinley Road, Knightswood, Glasgow, W. 3.
E. **Burman**, H., A.R.I.C., A.M.I.Chem.E.; 82 Dee Street, Riddrie, Glasgow, E. 1.
E. **Burnett**, Miss E. M., B.Sc.; c/o Mrs N. Matthews, 2 Carden Terrace, Aberdeen, Scotland.
E. **Burrows**, Dr Elsie M.; Hartley Botanical Laboratories, The University, Liverpool 3.
E. **Burton**, Dr Marie B.; 515 Tonbridge Road, Maidstone, Kent.
E. A. **Burtt**, B. L., B.Sc.; Royal Botanic Gardens, Edinburgh 4.
A. **Bush**, Dr S. F.; Dept. of Zoology, Natal University College, Pietermaritzburg, S. Africa.
E. **Butcher**, Dr R. W., B.Sc.; Culford House, Ewe Lamb Lane, Bramcote, Notts.
A. **Butler**, Dr C. G.; Rothamsted Experimental Station, Harpenden, Herts.
E. A. **Butler**, F. H. C., M.A., M.Sc.; Ravensmead, Keston, Kent.
A. **Buxton**, A. P.; Virus Research Institute, P.O. Box 49, Entebbe, Uganda.
E. A. **Buxton**, Lt.-Col. E. N., B.A., M.C.; Wallsgrove House, High Beach, Loughton, Essex.
A. **Buxton**, Prof. P. A., F.R.S.; London School of Hygiene, Keppel Street, London, W.C. 1.
E. **Cadman**, J. R.; 1 Park View, Barony, Nantwich, Cheshire.
E. **Caldwell**, Prof. J., D.Sc., Ph.D.; Dept. of Botany, University College of the South-West, Exeter.
E. **Callens**, Rev. Fr. Hubert; Jardin Gillet, Kisantu, Belgian Congo.
A. **Campbell**, B., Ph.D.; British Trust for Ornithology, 2 King Edward Street, Oxford.
E. **Campbell**, Miss M. S., F.L.S.; Easter Tegarmucha by Aberfeldy, Perthshire.
E. A. **Carpenter**, K.; 'Broad Gates', Bird Green, Beachamp Roding, Essex.
E. **Carson**, Dr G. P.; 2 Chesterton Hall Crescent, Cambridge.
A. **Carter**, Dr G. S.; Corpus Christi College, Cambridge.
E. A. **Carter**, J. E., M.A.; 38 Kennington Road, Fulwood, Preston, Lancs.
E. **Carter**, Dr Nellie; 23 Mount Side, Guildford, Surrey.
E. A. **Castell**, C. P., B.Sc.; 52 Graham Road, Wimbledon, London, S.W. 19.
E. **Chalklin**, Miss K. M., M.Sc.; Dept. of Botany, University Science Laboratories, South Road, Durham.
E. A. **Chambers**, Dr V. H., A.R.C.S.; 47 Westbourne Road, Luton, Beds.
E. A. **Champion**, Prof. H. G.; Imperial Forestry Institute, South Parks Road, Oxford.
A. **Chandler**, E. A., B.Sc.; Little Gate Rounds, Newdigate, Surrey.
E. **Chapman**, Mrs E. M. H.; c/o Forest Dept., Nicosia, Cyprus.
E. **Chapman**, P. C.; Charterhouse School, Godalming, Surrey.
E. **Chapman**, Prof. V. J., B.A., Ph.D.; Dept. of Botany, Univ. College, Auckland, New Zealand.
E. **Chapple**, J. F. G., F.L.S.; The Brackens, Nicholas Way, Northwood, Middlesex.
E. **Chater**, E. H., B.Sc.; Windover, Aberystwyth, Wales.
E. **Chatto**, A. E.; Weston, White Barn Farm, Elmstead, Colchester, Essex.
E. A. **Chear**, John, F.L.S.; 17 Elmwood, Welwyn Garden City, Herts.
A. **Chitty**, D. H.; Bureau of Animal Population, Botanic Garden, High Street, Oxford.
E. **Christie**, M. G., B.A.; E.A. Malaria Unit, P.O. Amani, Tanga, Tanganyika, E. Africa.
E. **Clapham**, Prof. A. R.; Botanical Dept., The University, Sheffield 10.
E. **Clark**, W. A., Ph.D.; Dept. of Botany, King's College, Newcastle-upon-Tyne 2.

E. **Clayton**, W. D.; Tanglewood, Plumpton, Sussex.
E. **Clowes**, Dr F. A. L.; Dept. of Botany, South Parks Road, Oxford.
A. **Colquhoun**, M. K.; Common Farm, Blackthorn, Bicester.
E. A. **Conder**, P. J.; Dale Fort Field Centre, Haverfordwest, Pembrokeshire.
E. **Conolly**, Miss A. P., M.A.; Botany Dept., University College, Leicester.
E. **Conway**, Mrs E.; Botany Dept., The University, Glasgow, W. 2.
E. **Conway**, Miss V. M., Ph.D.; The Nature Conservancy, 83–91 Victoria Street, London, S.W. 1.
E. **Coombe**, D. E.; Botany School, Downing Street, Cambridge.
E. **Cooper**, J. P., B.Sc.; Dept. of Agricultural Botany, The University, Reading.
E. **Cooper**, Prof. W. S.; 1421 Bluebell Avenue, Boulder, Colorado, U.S.A.
A. **Corbet**, P.S., B.Sc., F.R.E.S.; Dept. of Zoology, Downing Street, Cambridge.
E. **Cornish**, Miss M. W., B.Sc.; 63 Craigen Avenue, Croydon, Surrey.
E. A. **Coulson**, B. W. H.; The School, Oundle, nr Peterborough.
E. **Coulthard**, C. E., M.P.S.; 51 Henry Road, West Bridgford, Nottingham.
E. **Coupland**, R. T., Ph.D.; Dept. of Plant Ecology, University of Saskatchewan, Saskatoon, Canada.
A. **Cragg**, Prof. J. B., M.Sc.; Dept. of Zoology, Science Laboratories, South Road, Durham.
E. **Craig**, Miss A. M.; Fronheulog, New Road, Llanelly, Carmarthenshire.
A. **Cramp**, S., B.A.; 9 Queen Court, London, W.C. 1.
E. **Creber**, G. T.; 91 Headstone Lane, North Harrow, Middlesex.
E. **Crespin**, J. F., B.A.; The School, Dartington Hall, S. Devon.
E. **Crocker**, R. L., D.Sc.; Division of Soils, Hilgard Hall, University of California, Berkeley 4, California, U.S.A.
E. **Crowder**, Mrs A. A., B.A.; 25 Donview Road, Aberdeen.
E. **Croydon Natural History and Scientific Society**; 34 Raleigh Avenue, Wallington, Surrey.
E. **Crundwell**, A. C.; Dept. of Botany, The University, Glasgow, W. 2.
E. **Curtis**, Prof. J. T.; Botany Dept., Biology Building, University of Wisconsin, Madison 6, Wis., U.S.A.
E. **Curtis**, Miss W. M., Ph.D.; Botany Dept., University of Tasmania, Hobart, Tasmania.
E. **Daggash**, M.; c/o Forest Dept., Kaduna, N. Nigeria.
E. **Dalby**, D. H., B.Sc.; 108 Gordon Road, Camberley, Surrey.
A. **Dalgety**, C. T.; Lockerley Hall, Romsey, Hants.
E. A. **Dansereau**, Dr P.; Dept. of Botany, University of Michigan, Ann Arbor, Michigan, U.S.A.
E. A. **Darling**, F. F., D.Sc., Ph.D., F.R.S.E.; The Old Rectory, Lilley, Brightwalton, nr Newbury, Berks.
E. **Davenport**, E., B.Sc.; Hartley Botanical Laboratories, The University, Liverpool 3.
E. **Davey**, Miss A. J., M.Sc.; 20 Deiniol Road, Bangor, N. Wales.
E. **Davies**, Miss E. W., B.Sc.; Botany Dept., The University, Leeds.
E. A. **Davies**, J. Ll., M.A.; County Planning Dept., Clifton Road, Winchester.
A. **Davies**, L., Ph.D.; Dept. of Zoology, University Science Laboratories, South Road, Durham.
A. **Davies**, M. J., B.Sc.; Bureau of Animal Population, Botanic Garden, High Street, Oxford.
A. **Davies**, O. J. H.; The Oak House, Crossways, Shenfield, Essex.
E. **Davies**, Dr Wm.; Grassland Research Station, Drayton, Stratford-on-Avon, Warwicks.
E. **Davies**, W. C.; The Cawthron Institute, Nelson, New Zealand.
E. **Davis**, A. G., B.S.A., M.Sc.; Wye College, Ashford, Kent.
E. A. **Davis**, D. H. S.; Plague Research Laboratory, P.O. Box 1038, Johannesburg, S. Africa.
E. **Davis**, P. H., B.Sc., F.L.S.; Dept. of Botany, Royal Botanic Gardens, Edinburgh.
E. A. **Davis**, T. A. W.; South Mullock, Haverfordwest, Pembrokeshire.
A. **Davis**, W. B., Ph.D.; Box 254FE, College Station, Texas, U.S.A.
E. **Dawkins**, H. C., M.A.; c/o Forest Dept., Entebbe, Uganda.
A. **Day**, Dr J. H.; Dept. of Zoology, University of Cape Town, S. Africa.
A. **Delany**, M. J., B.Sc.; Dept. of Zoology, University College, Exeter.
E. **Dennis**, R. W. G., Ph.D.; The Herbarium, Royal Botanic Gardens, Kew, Surrey,
E. **De Rousset-Hall**, O., M.A.; 44 Great Bowden Road, Market Harborough, Leics.
A. **De Rousset-Hall**, Mrs P. J.; 44 Great Bowden Road, Market Harborough, Leics.

E. A. **Dice**, Lee R., Ph.D.; Institute of Human Biology, 1135 E, Catherine Street, Ann Arbor, Michigan, U.S.A.
E. **Dilnot**, Miss J., B.Sc.; 480 Liverpool Road, Birkdale, Southport, Lancs.
E. **Dimbleby**, G. W., M.A., D.Phil.; Imperial Forestry Institute, South Parks Road, Oxford.
E. A. **Diver**, Capt. C., C.B.E.; Nature Conservancy, 83–91 Victoria Street, London, S.W. 1.
A. **Dixon**, A. F. G.; 32 Lloyd Road, East Ham, London, E. 6.
A. **Donaldson**, R. P.; Royal Society for Protection of Birds, 82 Victoria Street, London, S.W. 1.
E. **Dony**, J. G., Ph.D.; 41 Somerset Avenue, Luton, Beds.
A. **Dowdeswell**, W. H., M.A.; 5 Kingsgate Street, Winchester.
A. **Driver**, P. M.; Warnless Cottage, Bond End, Upton St Leonards, Gloucester.
E. A. **Drummond**, R. B., B.Sc.; Herbarium, Royal Botanic Gardens, Kew, Surrey.
A. **Duffey**, E. A. G., B.Sc.; Bureau of Animal Population, Botanic Garden, High Street, Oxford.
A. **Duncan**, Miss A., B.Sc.; Royal Holloway College, Englefield Green, Surrey.
A. **Duncan**, A. B., B.A.; Lann Hall, Tynron, Dumfries.
A. **Dunnett**, G. M., B.Sc.; 30 Bonnymuir Place, Aberdeen, Scotland.
E. **Du Rietz**, Prof. Einar; Växtbiologiska Institutionen, Uppsala, Sweden.
E. A. **Dussart**, B. H., D.E.S.; Le Paraclet, par Boves, Somme, France.
E. **Ebuade-Iyamabo**, J. O.; Forest Headquarters, Ibadan, Nigeria.
A. **Edelstam**, Carl G.; Östermalmsgatan 61, Stockholm 5, Sweden.
A. **Edinburgh University Biological Society**, Royal Botanic Gardens, Edinburgh.
E. **Eggeling**, W. J., B.Sc., Ph.D.; Forest Office, Entebbe, Uganda.
E. **Elder**, N. L., M.A., F.R.G.S.; 43 McHardy Street, Havelock North, New Zealand.
E. A. **Elton**, Charles; Dept. of Zoological Field Studies, Botanic Garden, High Street, Oxford.
E. **Essex Field Club, The** (Essex Museum of Natural History, Romford Road, Stratford, London, E. 15).
E. **Evans**, Miss E. M., B.Sc.; c/o Mrs Foster, 12 Spring View Road, Sheffield 10.
E. **Evans**, E. Price; The Moorings, Glan-y-Mor Road, Deganwy, Llandudno Jnct., N. Wales.
A. **Evans**, F. C.; Institute of Human Biology, University of Michigan, 1135 E. Catherine Street, Ann Arbor, Michigan, U.S.A.
E. **Evans**, Dr G. C.; Botany School, Downing Street, Cambridge.
A. **Evans**, Dr Gwilym O.; Rothamsted Experimental Station, Harpenden, Herts.
E. **Falk**, P.; Tudor House, Horton Crescent, Rugby.
E. **Fanshawe**, D. B., B.A.; Forestry Station, Mazaruni, British Guiana.
E. **Fenton**, E. Wyllie, D.Sc.; 13 George Square, Edinburgh.
E. A. **Fenton**, G. R., B.A., B.Sc.; Church Farm, Gringley on the Hill, nr Doncaster.
A. **Fidler**, Dr J. H.; Ministry of Agriculture and Fisheries, University College of S. Wales and Mon., Cathays Park, Cardiff.
E. A. **Fincher**, F.; Randan Wood, Woodcote, Bromsgrove, Worcs.
E. A. **Fisher**, J. M.; Old Rectory, Ashton, Northants.
A. **Fitter**, R. S. R., B.Sc. (Econ.); Greyhounds, Burford, Oxon.
A. **FitzPatrick**, Mrs M. J.; 8 Cumberland Road, Barnes, London, S.W. 13.
E. **Fleming**, Dr G. W. T. H., F.L.S.; Barnwood House, Gloucester.
E. A. **Flemming**, W. J. W., B.A.; Soil Conservation, Public Works, Paeroa, New Zealand.
E. **Foggie**, A., B.Sc.; c/o Chief Conservator of Forests, P.O. Box 527, Accra, Gold Coast.
A. **Ford**, J.; Tsetse Research Dept., Shinyanga, Tanganyika Territory.
E. **Forman**, L. L., B.Sc.; 8 Glendale Avenue, Edgeware, Middlesex.
A. **Forster**, G. R., B.Sc.; Marine Biological Laboratory, Citadel Hill, Plymouth.
E. **Fourt**, D. F.; c/o Forest Research Station, Alice Holt Lodge, Wrecclesham, Farnham, Surrey.
E. **Frank**, Dr Erica M.; Box 31, Oak Glen Station, Lansing, Ill., U.S.A.
E. **Fraser**, D. A., B.A.; Forest Insect Laboratory, Sault Ste Marie, Ontario, Canada.
E. **Fraser**, G. K., M.A., D.Sc.; Macaulay Institute, Craigiebuckler, Aberdeen.
A. **Freeman**, Dr J. A.; Ministry of Food Infestation Division, 58 High Holborn, London, W.C. 1.
E. **Frost**, L. C., B.A.; The West Green, Poringland, Norwich, Norfolk.
E. **Frost**, Miss L. W., B.Sc.; 98 Bolton Road, Salford 6, Lancs.
A. **Frost**, Miss W. E.; The Ferry House, Far Sawrey, Ambleside, Westmorland.

A. **Froud**, M. D., B.Sc.; The College, Wye, Ashford, Kent.
E. **Fulford**, R. M.; Dept. of Botany, The University, Nottingham.
A. **Gabbutt**, P. D., B.Sc.; Dept. of Zoology, University College of S.W. England, Exeter.
E. **Galt**, R. W. C., B.Sc.; 20 Braid Farm Road, Edinburgh.
E. **Gams**, Dr Helmut; Schneeburggasse 67, Innsbruck-Hötting, Austria.
E. **Gardner**, Dr G.; School of Higher Commercial Studies, 535 Viger Avenue, Montreal, Canada.
E. **Gates**, L. F., B.A.; Dunholme Field Station, Dunholme Holt, Lincoln.
A. **Gauld**, D. T., Ph.D.; Dept. of Zoology, University College of the Gold Coast, Achimota, Gold Coast, W. Africa.
E. **Gayner**, J. S., M.R.C.S.; Hall Cottage, New Earswick, Yorks.
E. A. **Gensch**, R. H.; 105 Clark Avenue, Billings, Montana, U.S.A.
E. **George**, Miss B. N., B.A.; Grassland Research Station, Drayton, Stratford-on-Avon.
E. **Germain**, Dr R.; Institut National pour l'Étude Agronomique du Congo Belge, Yangambi, Congo Belge.
E. **Gibby**, Mrs A. N., B.Sc., A.R.I.C.; Prebend's Gate, Quarry Heads Lane, Durham.
E. **Gibson**, Miss C. M.; Trematon, 11 South Leigh Road, Havant, Hants.
A. **Gilbert**, O. J. W., B.Sc.; Zoology Dept., University College, Bangor, N. Wales.
E. **Gilbert-Carter**, H., M.A., M.B.; 'Thatcher', Holcombe, Dawlish, Devon.
E. A. **Gillett**, J. B., M.A.; 40 Pensford Avenue, Richmond, Surrey.
E. **Gillham**, Miss M. E.; 209 Gunnersbury Park, Ealing, London, W. 5.
E. **Gilliland**, Dr H. B.; Dept. of Botany, University of the Witwatersrand, Johannesburg, S. Africa.
E. **Gillman**, H., M.Sc.; District Agricultural Office, Bukoba, Tanganyika Territory.
E. **Gilmour**, J. S. L., M.A.; Director, University Botanical Gardens, Cambridge.
E. **Gilson**, Mrs M. R., Ph.D.; Sawrey House, Near Sawrey, Ambleside, Westmorland.
A. **Gilson**, H. Cary; The Ferry House, Far Sawrey, Ambleside, Westmorland (*Hon. Editor of Journal of Animal Ecology*).
E. **Gimingham**, C. H., B.A., Ph.D.; Dept. of Botany, The University, Old Aberdeen.
E. A. **Glasgow and Andersonian Nat. Hist. and Microscopical Soc.**; Societies' Rooms, Royal Technical College, Glasgow.
A. **Glasgow**, Dr J. P.; EATTRRO, P.O. Maseno, via Kisumu, Kenya.
E. A. **Glover**, Major P. E., M.Sc.; c/o EATTRRO, P.O. Box 2141, Nairobi, Kenya.
A. **Godfrey**. Miss G. K.; St Anne's Society, Musgrave House, 1 South Parks Road, Oxford.
E. **Godward**, Dr Maud, B.E.; 8 Deyncourt Gardens, Upminster, Essex.
E. A. **Godwin**, H., Sc.D., F.R.S.; Botany School, Cambridge (*Hon. Editor, Journal of Ecology*).
E. A. **Good**, Prof. R. D'O., M.A., ScD.; Botanical Dept., University College, Hull.
E. **Goodall**, D. W., B.Sc., Ph.D., D.I.C.; Botany School, Melbourne University, Melbourne, N. 3, Australia.
A. **Goodbody**, I. M., B.A.; Natural History Dept., Marischal College, Aberdeen.
A. **Goodhart**, C. B.; 28 St Margaret's Road, Cambridge.
E. **Goodman**, G. T., B.Sc.; 120 Pendre, Bridgend, Glamorgan.
E. **Goodwin**, Du Wayne, L., M.S.; Botany Dept., Washington State College, Pullman, Washington, U.S.A.
E. **Gorham**, Eville, M.Sc.; Dept. of Botany, University College, Gower Street, London, W.C. 1.
A. **Gradwell**, G. R., M.A.; Hope Dept. of Entomology, University Museum, Oxford.
E. **Green**, P. S., B.Sc.; Royal Botanic Garden, Edinburgh 4.
E. **Greenway**, P. J., F.L.S.; East African Herbarium, P.O. Box 5166, Nairobi, Kenya Colony.
E. **Greig-Smith**, T.; Dept. of Botany, University College of North Wales, Bangor.
E. **Gröntved**, Johannes; Botanisk Museum, Gothersgade 130, Copenhagen, K, Denmark.
E. **Grose**, J. D.; Downs Edge, Liddington, nr Swindon, Wilts.
E. **Grove**, A. T., M.A.; 2 Princess Road, Evesham, Worcs.
A. **Gudjonsson**, T. V., M.Sc.; P.O. Box 754, Reykjavik, Iceland.
E. A. **Gudmundsson**, Dr F.; Náttúrugripasafnid, P.O. Box 532, Reykjavik, Iceland.
E. A. **Haddow**, Dr A. J., M.B., Ch.B., B.Sc., D.P.M. & H.; Yellow Fever Research Institute, Field Box 49, Entebbe, Uganda.
A. **Hague**, Kathleen M., B.Sc.; Loreto Club, 14 Blandford Street, London, W. 1.

A. **Hairston**, N. G., M.A., Ph.D.; Dept. of Zoology, University of Michigan, Ann Arbor, Michigan, U.S.A.
E. **Halket**, Miss A. C., D.Sc.; Tupra, Elstead, nr Godalming, Surrey.
E. **Hall**, R. H.; 2 Hartington Terrace, West Road, Buxton, Derbyshire.
E. **el-Halwagy**, R., B.Sc.; Dept. of Botany, University College, Gower Street, London, W.C. 1.
E. **Hambler**, D. J., B.Sc.; 59 Jersey Road, Strood, Kent.
A. **Hamerstrom**, Dr F.; Plainfield, Wisconsin, U.S.A.
E. **Harberd**, D. J., M.Sc.; Scottish Soc. for Research in Plant Breeding, Corstorphine, Edinburgh 12.
A. **Hardy**, Prof. A. C., M.A., D.Sc., F.R.S.; University Dept. of Zoology, Oxford.
E. **Hare**, C. Leighton, M.Sc., Ph.D.; 21 Ashridge Avenue, North Bournemouth.
A. **Harker**, Miss J. E., Ph.D.; Zoology Dept., The University, Manchester 13.
E. **Harley**, J. L., M.A., D.Phil.; University Dept. of Botany, South Parks Road, Oxford.
E. **Harper**, J. L., B.Sc.; University Dept. of Agriculture, Parks Road, Oxford.
E. **Harper**, P. C., B.Sc.; Edinburgh and E. of Scotland College of Agriculture, 13 George Square, Edinburgh 9.
E. **Harris**, C. M.; Woodland Management Association Ltd., Lodge Park, Aldsworth, Glos.
A. **Harris**, L. F.; 30 Ellis Avenue, Rainham, Essex.
A. **Harris**, Prof. T. M., M.A., Sc.D., F.R.S.; Botany Dept., The University, Reading.
A. **Hartland-Rowe**, R. C. B., B.Sc.; Dept. of Biology, Makerere College, P.O. Box 262, Kampala, Uganda, E. Africa.
A. **Hartley**, Rev. P. H. T., B.Sc.; Badingham Rectory, Woodbridge, Suffolk.
E. A. **Harvey**, Prof. L. A., M.Sc.; Dept. of Zoology, University College of S.W. England, Exeter, Devon.
E. **Haywood**, J., B.Sc.; 6 Pendre, Bridgend, Glamorgan.
E. **Heddle**, R. G., M.A., B.Sc.; Edinburgh and E. of Scotland College of Agric., 13 George Square, Edinburgh.
E. **Hemsley**, J. H., B.Sc.; Herbarium, Royal Botanic Gardens, Kew, Surrey.
E. **Henderson**, A. G., B.Sc.; North Craigton, Culter, Aberdeenshire, Scotland.
A. **Henderson**, Miss M.; 44 Higher Bebington Road, Bebington, Cheshire.
E. A. **Hepburn**, I., M.A.; 2 Old Dryden House, Oundle, Peterborough.
E. **Hepper**, F. N., B.Sc.; Herbarium, Royal Botanic Gardens, Kew, Surrey.
E. A. **Heslop-Harrison**, J., M.Sc., Ph.D.; Botany Dept., University College, Gower Street, London, W.C. 1.
E. A. **Heslop-Harrison**, Prof. J. W., F.R.S.; Agricultural Dept., King's College, Newcastle-upon-Tyne 1.
A. **Hewer**, H. R., A.R.C.S., M.Sc.; Dept. of Zoology and Applied Entomology, Imperial College, London, S.W. 7.
E. **Hewetson**, C. E.; Raipur, Madhya, Pradesh, India.
E. **Hewitt**, Miss M. S.; 92 Park Avenue, Kingston-upon-Hull, Yorks.
E. **Heywood**, V. H., B.Sc.; Botany School, Downing Street, Cambridge.
E. A. **Hinchcliffe**, R., B.A.; Belmont Station, Box 455, Broken Hill, N.S.W., Australia.
A. **Hobart**, J., B.Sc.; Dept. of Agricultural Zoology, University College, Bangor.
A. **Hobby**, B. M., M.A., D.Phil.; University Museum, Oxford.
A. **Hodgkin**, E. P.; 6 Princes Street, Mosman Park, Western Australia.
E. **Holch**, Dr A. E.; Dept. of Botany, University of Denver, Colorado, U.S.A.
E. **Hole**, Miss D. R., B.Sc.; Rousdon, Cutbush Lane, Shinfield, Reading.
A. **Holme**, N. A., B.A.; The Laboratory, Citadel Hill, Plymouth.
E. A. **Holmes**, P. F., M.A.; Malham Tarn Field Centre, nr Settle, Yorks.
E. **Holttum**, Prof. R. E., M.A.; University of Malaya, Cluny Road, Singapore, 10, Malaya.
E. A. **Holway**, P. H.; Colfe's Grammar School, Lewisham, London, S.E. 13.
E. **Hope-Simpson**, J. F., D.Phil.; Dept. of Botany, The University, Bristol 8.
E. **Hopkins**, B., B.Sc.; 63 Kingsway, Pendlebury, Lancs.
E. A. **Hornby**, H. E., F.R.C.V.S.; Poole Farm, Hartley, S. Rhodesia.
E. **Horne**, F. R., M.A.; Hill Farm, Lolworth, Cambs.
A. **Horridge**, G. A., B.A.; St John's College, Cambridge.
E. **Hoyle**, A. C., M.A.; 45 Green Road, Headington, Oxford.
E. **Hubbard**, C. E.; 60 Albury Avenue, Isleworth, Middlesex (*Hon. Treasurer*; receives subscriptions).

A. **Huddart**, B. J.; Shirley House, Marsh Lane, Taplow, Bucks.
E. **Hughes**, F. E., B.A.; c/o Westminster Bank, High Street, Oxford.
E. **Hughes**, R. E., M.A., Ph.D.; School of Agriculture, Downing Street, Cambridge (*Hon. Secretary*).
A. **Hume**, Maj. C. W.; 284 Regent's Park Road, Finchley, London, N. 3.
A. **Humphries**, Miss D. A., B.Sc.; Butt Lane, Milton, Cambs.
E. **Hyde**, H. A., M.A.; National Museum of Wales, Cardiff, S. Wales.
A. **Hynes**, H. B. N., Ph.D.; Dept. of Zoology, The University, Liverpool.
E. **Irvine**, F. R., D.Sc.; 32 Tavistock Square, London, W.C. 1.
E. **Ivens**, G. W.; Mariposa, Longwell Green, nr Bristol.
E. **Ivimey-Cook**, R. B., B.Sc.; Westra Lodge, Dinas Powis, Glamorgan.
E. **Jackson**, A. C., B.Sc.; 37 Lynton Avenue, Chanterlands Avenue, Hull, Yorkshire.
E. A. **Jackson**, C. H. N., Ph.D.; Dept. of Tsetse Research, Shinyanga, Tanganyika Territory.
E. A. **Jackson**, D. S., B.A.; c/o National Bank of New Zealand, Rotorua, New Zealand.
E. **Jackson**, G., B.Sc.; 4 Rivelin Park Road, Sheffield 6.
E. **Jackson**, J. K., B.Sc.; c/o Research Division; Wad Medani, Anglo-Egyptian Sudan.
E. **Jackson**, R. M., B.Sc.; Dept. of Botany, The University, Nottingham.
A. **Jacob**, F. H.; Plant Pathology Laboratory, Milton Road, Harpenden, Herts.
A. **Jameson**, E. W., Jr., B.S., M.A.; Division of Zoology, University of California, Davis, California, U.S.A.
E. **Jameson**, J. H., M.A.; 25 Radnor Road, Handsworth, Birmingham 20.
E. **Jane**, Prof. F. W., D.Sc., F.L.S.; Highfield, Egham Hill, Englefield Green, Surrey.
E. **Jaques**, Miss M.; Egmont, St James Lane, Winchester, Hants.
E. A. **Jarrett**, T., Dept. Agric.; c/o P.O. Box 2141, Nairobi, Kenya, East Africa.
A. **Jary**, S. G.; South-Eastern Agricultural College, Wye, Ashford, Kent.
Jennings, O. E.; Carnegie Museum, Pittsburg, Pa., U.S.A. (*Hon. Life-Member*).
E. **Jensen**, H. A. P., M.A.; The Nature Conservancy, 91 Victoria Street, London, S.W. 1.
E. **Jermy**, A. C.; 'Tandem', East Avenue, Brundall, Norfolk.
E. **Johnson**, C. S. E., B.A.; Conservation Officer, P.O. Dawson's, S. Rhodesia.
A. **Johnson**, D. S., B.A.; Dept. of Zoology, Bedford College, London, N.W. 1.
E. A. **Johnson**, F. M., A.M.I.Mech.E., A.M.I.M.I.; 22 Bellevue Crescent, Duffield, nr Derby.
E. **Jones**, Dr E. W.; Imperial Institute of Forestry, Oxford.
E. **Jones**, F. R.; 19 Windermere Road, Streatham, London, S.W. 16.
E. **Jones**, Miss G. M.; The Cottage, Wraysbury, Bucks.
A. **Jones**, N. S., M.Sc.; Marine Biological Station, Port Erin, Isle of Man.
A. **Jones**, R. J., B.A.; Whitgift School, Haling Park, South Croydon, Surrey.
E. **Jones**, Miss V., B.Sc.; Botany Dept., University College of North Wales, Bangor.
A. **Jordan**, A. M., B.Sc.; 'Buckland', Hollow Lane, Ramsey, Hunts.
E. **Kassas**, M. A. F. El-, M.Sc., Ph.D.; Faculty of Science, Fouad I University, Cairo, Egypt.
E. **Keay**, R. W. J., M.A., F.L.S.; 40 Fairfax Road, Teddington, Middlesex.
A. **Keir**, R. S., B.Sc.; 51 Clincort Road, Glasgow, S. 2.
A. **Kellas**, Miss L. M.; 63 Carlton Place, Aberdeen.
A. **Kellen**, A. K. I., B.Sc.; 151 Glebelands, Hakin, Milford Haven, Pembrokeshire.
A. **Kendeigh**, S. C., Ph.D.; Vivarium Building, University of Illinois, Wright and Healey Streets, Champaign, Illinois, U.S.A.
A. **Kennington**, G. S., Ph.D.; Dept. of Biology, Lawrence College, Appleton, Wisconsin, U.S.A.
A. **Kenrick**, W. E., M.A.; Metchley Abbey, Harbourne, Birmingham 17.
A. **Kettle**, D. S., M.Sc.; Dept. of Zoology, West Mains Road, Edinburgh 9.
E. **King**, J., B.Sc.; Edinburgh and E. of Scotland College of Agriculture, Sourhope Farm, Yetholm, Kelso, Roxburghshire.
A. **King**, J. A.; Roscoe B. Jackson Memorial Laboratory, Bar Harbor, Maine, U.S.A.
A. **Kitching**, J. A., M.A.; Zoology Dept., The University, Bristol 8 (*Vice-President*).
E. **Klika**, Prof. Jaromír, Ph.D.; Ecole polytechnique, Praha,—Kosire 333, Czechoslovakia.
A. **Knight-Jones**, E. W., B.Sc., D.Phil.; Marine Biological Station, Bangor, N. Wales.
E. **de Kock**, Dr P. C., M.Sc.; 10 Chanonry, Old Aberdeen.
A. **Kristensen**, Dr I.; Zoological Station, Den Helder, Holland.

A. **Krogstad**, B. O., Asst. Prof.; Dept. of Biology, St Olaf College, Northfield, Minnesota, U.S.A.
A. **Krumholz**, L. A., Ph.D.; P.O. Box 2105, Oak Ridge, Tennessee, U.S.A.
A. **Lack**, D., Sc.D.; Edward Grey Inst. of Field Ornithology, Dept. of Zoological Field Studies, Botanic Garden, High Street, Oxford.
E. **Lambert**, Miss J. M., Ph.D.; Newnham College, Cambridge.
E. **Landon**, F. H.; c/o Dept. of Forestry, Kuala Lumpur, Malaya.
A. **Larkin**, Prof. P. A., M.A.; Dept. of Zoology, University of British Columbia, Vancouver, B.C., Canada.
A. **Laurie**, Miss E. M. O., M.Sc.; British Museum (Nat. Hist.), Cromwell Road, London, S.W. 7.
E. **Laurie**, M. V., M.A., O.B.E.; Forest Research Station, Alice Holt, Farnham, Surrey.
E. **Lavender**, J. H., B.Sc., A.R.C.S.; 1 Manor Road, Christchurch, Hants.
E. **Lawrie**, J. J., B.Sc.; 19 Fullerton Drive, Troon, Ayrshire.
E. A. **LeCren**, E. D.; The Ferry House, Far Sawrey, Ambleside, Westmorland.
E. **Lee**, Major O. M., F.L.S.; School of Agriculture, Serdang, Selangor, Malaya.
A. **Lemare**, D. W., B.A.; Fisheries Dept., Singapore, Malaya.
E. **Leonard**, Mrs V. P.; c/o Lloyds Bank, Cambridge.
E. A. **Leston**, D., F.Z.S., F.R.E.S.; 44 Abbey Road, London, N.W. 8.
E. A. **Lewis**, C. B.; Museum of the Institute of Jamaica, Kingston, Jamaica, B.W.I.
A. **Lewis**, D. J., M.A.; Agricultural Research Service, Wad Medani, Anglo-Egyptian Sudan.
E. **Lewis**, J., B.Sc.; 52 Southfield Road, North Harrow, Middlesex.
E. A. **Lewis**, J. R., B.Sc.; Dept. of Zoology, University College of Wales, Cambrian Street, Aberystwyth.
E. A. **Lewis**, J. Spedan; Leckford Abbas, Stockbridge, Hants.
E. **Lewis**, Miss P., B.Sc., F.L.S.; Herbarium, Royal Botanic Gardens, Kew, Surrey.
E. **Leyton**, Dr L.; Imperial Forestry Institute, South Parks Road, Oxford.
E. **Libbey**, R. P., B.Sc.; Laurel Villa, 143 Gaywood Road, King's Lynn, Norfolk.
E. **Lind**, Miss E. M., B.Sc., Ph.D.; Makerere College, P.O. Box 262, Kampala, Uganda, E. Africa.
A. **Linn**, I. J., B.Sc.; Dept. of Zoology, University College, Exeter.
E. A. **Lloyd**, L. C.; Shackerley, Wenlock Road, Shrewsbury, Shrops.
E. **Lodge**, Miss S. M., B.Sc.; Marine Biological Station, Port Erin, Isle of Man.
E. A. **London Natural History Society**; c/o C. P. Castell, 52 Graham Road, Wimbledon, London, S.W. 19.
E. **Löve**, Dr Askell, Dept. of Botany, University of Manitoba, Winnipeg, Canada.
E. **Loveless**, A. R., Ph.D.; Dept. of Botany, University College of the W. Indies, Mona, St Andrew, Jamaica, B.W.I.
E. A. **Lovett**, M., B.Sc., F.R.I.C., F.Inst.S.P.; Yorkshire Ouse River Board, 21 Park Square South, Leeds 1.
A. **Lowe**, Miss R. H., B.Sc.; Fisheries Research Laboratory, P.O. Box 343, Jinja, Uganda, E. Africa.
E. **Lüdi**, Dr W.; Gartenstrasse 12, Zollikon, Zürich, Switzerland.
A. **Lumsden**, W. H. R., B.Sc., M.B.; Virus Research Institute, P.O. Box No. 49, Entebbe, Uganda, E. Africa.
E. **Lund**, J. W. G., M.Sc., Ph.D.; Freshwater Biological Assoc., The Ferry House, Far Sawrey, Ambleside, Westmorland.
A. **Lutz**, Dr Bertha; National Museum, Quinta de Boa Vista, Rio de Janeiro, Brazil.
A. **Macan**, T. T.; Stevney, Outgate, Ambleside, Westmorland.
E. A. **Macfadyen**, A.; Dubber's Field, Old Boars Hill, Oxford.
A. **McHardy**, J. W., B.Sc.; Dept. of Agric. and Forest Zoology, 10 George Square, Edinburgh 8, Scotland.
A. **Mackenzie**, J. M. D., F.Z.S.; Greyfriars, Greyfriars Garden, St Andrews, Scotland.
A. **MacLagan**, D. S., D.Sc., Ph.D., F.R.E.S.; West of Scotland Agricultural College, 6 Blythswood Square, Glasgow, C 2.
E. **McLean**, Prof. R. C., M.A., D.Sc.; University College, Newport Road, Cardiff, S. Wales.
E. **MacLeay**, K. N. G., B.Sc.; Gordon Memorial College, Khartoum, Anglo-Egyptian Sudan.
E. **Macleod**, Dr Anna M.,; Heriot-Watt College, Edinburgh 1.
A. **MacLeod**, J., D.Sc.; Veterinary Laboratory, New Haw, Weybridge, Surrey.
E. **McLuckie**, J., D.Sc.; Dept. of Botany, The University, Sydney, Australia.

A. **MacLulich**, D. A., Ph.D.; 15 Bellwood Avenue, Ottawa, Ontario, Canada.
E. A. **MacNae**, W., B.Sc.; Dept. of Zoology, Rhodes University, Grahamstown, S. Africa.
A. **Macpherson**, Miss B., B.Sc.; Bureau of Animal Population, Botanic Garden, High Street, Oxford.
E. A. **McVean**, D. N., B.Sc., B.Sc. (Agric.) N.D.A.; Nature Conservancy, 12 Hope Street, Edinburgh.
A. **Madsen**, H., M.Sc.; Jagtraådets Vildtbiologiske Undersøgelser, Universitetsparken 3, København, Denmark.
E. **Major**, J.; Division of Soils, University of California, Berkeley, California, U.S.A.
E. **Mangham**, Prof. S., M.A.; University College, Southampton.
A. **Mann**, K. H., B.Sc.; Dept. of Zoology, The University, Reading.
A. **Marples**, Prof. B. J.; The Museum, Dunedin, New Zealand.
E. **Marsden-Jones**, E. M.; Close Cottage, Littleton Panell, nr Devizes, Wilts.
E. **Mason**, E. W.; Inglenook, 63 King's Road, Richmond, Surrey.
A. **Matheson**, C., M.A., B.Sc.; Dept. of Zoology, National Museum of Wales, Cardiff.
E. **Matthews**, Prof. J. R., M.A.; Dept. of Botany, The University, Old Aberdeen.
E. **Meikle**, R. D., B.A., LL.B.; Herbarium, Royal Botanic Gardens, Kew, Surrey.
A. **Mellanby**, Dr K.; The University, Ibadan, Nigeria.
E. A. **Melville**, R., Ph.D.; Herbarium, Royal Botanic Gardens, Kew, Surrey.
E. **Merton**, L. F. H., B.A.; BM/XKEG, London, W.C. 1.
E. **Messeri**, Prof. Albina; Via Bolognese 43, Firenze, Italy.
E. **Metcalfe**, Dr G., M.A.; Botany Dept., King's College, Strand, London, W.C. 2.
E. A. **Meyerriecks**, A. J.; 119–20, 146th Street, South Ozone Park 20, New York, U.S.A.
E. A. **Michelmore**, A. P. G., B.A.; Saffron Close, Chudleigh, S. Devon.
A. **Middleton**, A. D.; I.C.I. Game Services, Burgate Manor, Fordingbridge, Hants.
E. A. **Middleton**, Dr A. R.; Biological Labs., University of Louisville, Louisville, Kentucky, U.S.A.
E. **Migahid**, A. M.; Botany Dept., Faculty of Science, Fouad I University, Abbassieh, Cairo, Egypt.
E. A. **Miller**, R. S., B.A.; Harvard University, Biological Labs., 16 Divinity Avenue, Cambridge 38, Mass., U.S.A.
A. **Milne**, Dr A., M.A.; Dept. of Agriculture, King's College, Newcastle-upon-Tyne 2.
E. A. **Milne-Redhead**, E. W. B. H., M.A.; The Herbarium, Royal Botanic Gardens, Kew, Surrey.
E. **Mirams**, R. V., M.Sc.; 555 Manukau Road, Epsom, Auckland, New Zealand.
E. **Misra**, Dr R.; Dept. of Botany, University of Saugor, Saugor, Central Provinces, India.
E. **Mitchell**, G. F., M.A.; Dept. of Irish Archaeology, Trinity College, Dublin, Eire.
E. **Mohan**, N. P., M.A., B.Sc.; Chief Conservator of Forests, Himachal Dradesh Secretariat, Simla, India.
E. **Montasir**, Professor Abd El-Halim, Ph.D., M.S.; Faculty of Science, Ibrahim University, Orman, Giza, Egypt.
A. **Montford**, H. M., B.Sc.; 23 Mount Side, Guildford, Surrey.
A. **Moon**, Prof. H. P., M.A.; Dept. of Zoology, University College, Leicester.
E. **Mooney**, H. F., C.I.E., O.B.E., Sc.D., F.L.S.; British Middle East Office, British Legation, Beirut, Lebanon.
E. A. **Moore**, Barrington; Stone Acre, Corfe, Taunton.
E. **Moore**, Mrs M., B.Sc.; 17 Staplehurst Road, Hall Green, Birmingham 28.
A. **Moore**, N. W., B.A.; The Nature Conservancy, Furzebrook Research Station, Wareham, Dorset.
E. **Moore**, R. M., M.Sc.; Division of Plant Industry, C.S.I.R.O., Canberra, A.C.T., Australia.
A. **Morley**, B. D. W., B.A., F.L.S.; Institute of Animal Genetics, West Mains Road, Edinburgh 9.
E. A. **Moynahan**, E. J., M.R.C.S.; Wayside, Jordans, Beaconsfield, Bucks.
A. **Muir**, R. C.; Zoology Dept., Downing Street, Cambridge.
A. **Mundie**, J. H., B.Sc.; Imperial College Field Station, Silwood Park, Sunningdale.
A. **Murphy**, D. H.; Zoology Dept., South Road, Durham.
A. **Neal**, E. G., B.Sc.; 2 Bishop's Mead, Kingston Road, Taunton.
E. **Neales**, T. F.; Worcester College, Oxford.
A. **Nelmes**, E. M., B.A.; 27 Westbourne Avenue, Acton, London, W. 3.
E. **Nelmes**, Miss S.; 48 Defoe Avenue, Kew, Surrey.

E. **Newbould**, P. J.; 27 The Poplars, Ferring-by-Sea, Sussex.
E. A. **Newman**, Leslie F., M.A.; 45 London Road, Bishop's Stortford, Herts.
E. **Newton**, Miss L. M., B.Sc.; British Museum (Nat. Hist.), Cromwell Road, London, S.W. 7.
E. A. **Newton**, Prof. Lily, M.Sc., Ph.D.; Dept. of Botany, University College of Wales, Aberystwyth, Wales.
A. **Newton**, Dr R. G.; 4 Walden Road, Welwyn Garden City.
A. **Nichols**, J. E., Ph.D.; Dept. of Agriculture, University College of Wales, Aberystwyth.
A. **Nicholson**, E. M.; 13 Upper Cheyne Row, London, S.W. 3.
E. **Nicholson**, I. A., B.Sc.; Grassland Dept., N. Scotland College of Agriculture, 41½ Union Street, Aberdeen.
E. A. **Nielsen**, C. O., D.Phil.; Naturhistorisk Museum, Aarhus, Denmark.
E. **Norman**, M. J. T., B.Sc.; Grassland Research Station, Hurley, nr. Maidenhead, Berks.
A. **Norris**, K. R., M.Sc.; C.S.I.R.O. Entomology Division, P.O. Box 109 City, Canberra, A.C.T., Australia.
E. **Northumberland, Durham & Newcastle-on-Tyne Nat. Hist. Soc.**; Hancock Museum, Barras Bridge, Newcastle-on-Tyne 2.
E. **O'Connor**, Miss W. M. T., B.Sc.; Hartley Botanical Laboratories, The University, Liverpool 3.
E. **Oliver**, W. R. B., D.Sc.; 26 Ventnor Street, Seatown, Wellington, E. 5, New Zealand.
A. **Omer-Cooper**, Prof. J., M.A., M.Sc.; Rhodes University College, Grahamstown, S. Africa.
E. A. **Orr**, H. R.; Technical College, Longport Street, Canterbury.
E. **Orr**, M. Y.; 21 Blinkbonny Grove, Edinburgh 4.
E. **Osborn**, Prof. T. G. B.; University Dept. of Botany, South Parks Road, Oxford.
E. **Osmaston**, H., M.A.; Forest Office, Fort Portal, Uganda, E. Africa.
E. **Osvald**, Prof. K. Hugo; Royal Agricultural College, Uppsala 7, Sweden.
E. **Ovington**, J. D., Ph.D.; Nature Conservancy, 83–91 Victoria Street, London. S.W. 1.
A. **Pallant**, D., B.Sc.; 8 Andover Road, Southsea, Hants.
E. A. **Park**, Dr O.; Zoological Dept., Northwestern University College of Liberal Arts, Evanston, Ill., U.S.A.
E. **Parke**, Dr Mary; The Laboratory, Citadel Hill, Plymouth.
E. **Parker**, R. E., B.Sc.; Dept. of Botany, University College of North Wales, Bangor.
E. **Parkinson**, Mrs M., M.A.; 13 Southernhay West, Exeter.
A. **Parry**, D. A., Ph.D.; King's College, Cambridge.
Paterson, Mrs H. M.; 61 Smarts Road, Gravesend, Kent (*Associate Member*).
A. **Paulson**, C. W. G.; c/o Monotype Corporation, Ltd., Salfords, Redhill, Surrey.
A. **Peacock**, Prof. A. D., D.Sc., F.R.S.E.; University College, Dundee.
A. **Peake**, J. F.; 17 Tillet Road, Norwich.
E. **Pearsall**, Prof. W. H., F.R.S.; Botany Dept., University College, Gower Street, London, W.C. 1.
E. A. **Pearson**, J., D.Sc.; Tasmanian Museum and Art Gallery, Hobart, Tasmania.
E. **Pearson**, M. C., B.Sc.; 17 Norman Road, Sale, Manchester.
E. **Penston**, Dr Norah L., F.L.S.; Bedford College, Regent's Park, London, N.W. 1.
A. **Pentelow**, F. T. K.; Old Slade Lane, Iver, Bucks.
A. **Percival**, Prof. E.; Canterbury University College, Christchurch, New Zealand.
A. **Perkins**, E. J.; Post Office, Cross Keys, Hereford.
E. **Perraton**, C. J., B.A.; Munro College, Jamaica, B.W.I.
E. **Perrin**, R. M., B.A.; School of Agriculture, Cambridge.
E. **Perring**, F. H., B.A.; 59 Warkworth Terrace, Cambridge.
E. **Perry**, R. A., B.Sc.; 7 Quick Street, Ainslie, Canberra City, A.C.T., Australia.
E. **Petch**, C. P., M.A., M.B.; Sundial House, North Wootton, King's Lynn, Norfolk.
E. **Peterken**, J. H. G., F.L.S.; 73 Forest Drive East, Leytonstone, London, E. 11.
E. A. **Phillips**, Prof. J. F. V.; University College of the Gold Coast, Achimota, P.O., Accra, B.W. Africa.
E. **Phillips**, Miss M. E., M.Sc.; Dept. of Botany, The University, Manchester 13.
E. **Pichi-Sermolli**, Prof. R.; Istituto Botanico dell' Universita, Via Lamarmora 4, Firenze, Italy.
E. **Pielou**, E. C. (Mrs), B.Sc.; c/o Dominion Entomological Lab., Summerland, British Columbia.
A. **Pielou**, Dr D. P.; Dominion Entomological Laboratory, Summerland, British Columbia.
E. **Piemeisel**, R. L.; P.O. Box 826, Twin Falls, Idaho, U.S.A.

E. **Pigott**, C. D., B.A.; Clevedon, Harestone Hill, Caterham, Surrey.
A. **Pitelka**, F. A., Ph.D.; Museum of Vertebrate Zoology, University of California, Berkeley 4, California, U.S.A.
E. **Pitman**, P. B., B.Sc.; 3 Beverley Gardens. Ensbury Park, Bournemouth.
E. **Poel**, Dr L. W.; Dept. of Botany, The University, St Andrews.
E. **Polunin**, Prof. N., D.Phil., D.Sc.; Gray Herbarium, Harvard University, 79 Garden Street, Cambridge, Mass., U.S.A.
E. A. **Poore**, M. E. D.; The Rectory, Landbeach, Cambs.
E. **Pope**, Miss E. C., M.Sc.; The Australian Museum, College Street, Sydney, Australia.
E. A. **Potts**, W. H., M.A.; 45 Green Moor Link, Windermere Hill, London, N. 21.
E. A. **Pough**, R. H.; American Museum of Natural History, Central Park West at 79th Street, New York 24, N.Y., U.S.A.
E. **Powell**, Miss Doris, M.Sc.; Aldersyde, Reigate, Surrey.
E. A. **Powell**, H. T., B.Sc.; Marine Station, Millport, Isle of Cumbrae, Scotland.
A. **Pradhan**, Dr S.; Entomology Division, Indian Agricultural Research Institute, New Delhi, India.
E. A. **Praeger**, Dr R. Lloyd; Royal Irish Academy, 19 Dawson Street, Dublin.
E. **Pratt**, Dr C. A.; Botany Dept., Imperial College of Science and Technology, London, S.W. 7.
A. **Preston**, F. W., Preston Laboratories, Box 847, Butler, Pennsylvania, U.S.A.
A. **Price**, Miss K. L. H.; Hillside, Headington Hill, Oxford.
A. **Price Jones**, Dr D.; Fernhurst, nr Haslemere, Surrey.
A. **Prideaux**, R. C.; Claigan, Dunvegan, Isle of Skye.
E. **Prime**, C. T., M.A., Ph.D., F.L.S.; 147 Upper Selsdon Road, Sanderstead, S. Croydon, Surrey.
E. **Proctor**, M. C. F., B.A.; Botany School, Downing Street, Cambridge.
E. **Puri**, Dr G. S.; Forest Research Institute, P.O. New Forest, Dehra Dun (U.P.), India.
A. **Putnam**, C. D., B.A.; 14 Maids' Causeway, Cambridge.
E. **Quist-Arcton**, E. A.; Brasenose College, Oxford.
A. **Radway Allen**, K.; P.O. Box 202, Fisheries Laboratory, Marine Dept., Wellington, New Zealand.
E. **Raggio**, M.; 25 de Mayo 316, Esc. 2, Piso 1. Buenos Aires, Argentina.
E. **Rains**, A. B., B.Sc.; 28 Vicarage Lane, Humberstone, Leicester.
E. **Ramsbottom**, J., M.A., O.B.E.; British Museum (Nat. Hist.), Cromwell Road, London, S.W. 7.
A. **Rand**, R. W., B.Sc.; c/o Union Govt., Guano Is., 32 Riebeck Street, Cape Town, S. Africa.
E. **Ranwell**, D. S., B.Sc.; Dept. of Botany, University College of North Wales, Memorial Buildings, Bangor, Caern.
E. **Ratcliffe**, D. A., B.Sc.; 72 Newton Road, Carlisle.
A. **Ratcliffe**, F. N., B.A.; Council for Scientific and Industrial Research, P.O. Box 109, Canberra, A.C.T., Australia.
A. **Raw**, Frank, B.Sc.; Rothamsted Experimental Station, Harpenden, Herts.
A. **Raymont**, Prof. J. E. G., B.Sc., A.M.; Dept. of Zoology, University College, Southampton.
E. **Rees**, J., B.A., M.Sc.; N.A.A.S., Min. of Agriculture and Fisheries, University College, Cardiff.
E. **Rees**, T. Kenneth; Board of Trade, Neville House, Page Street, London, S.W. 1.
E. **Rees**, W. J., Ph.D.; Botany Dept., The University, Edgbaston, Birmingham 15.
E. A. **Rees-Wright**, Rev. Prof. W., Ph.D.; Dept of Biology, Memorial University College, St John's, Newfoundland.
E. **Regel**, Dr C.; University College of Arts and Sciences, Baghdad, Iraq.
E. A. **Reid**, D. A., B.Sc.; 19 High Street, Leighton Buzzard, Beds.
A. **Reid**, D. M.; Science Schools, Harrow-on-the-Hill, Middlesex.
A. **Reid**, R. E. H., B.Sc.; Pentryn, Bois Lane, Chesham Bois, Bucks.
E. A. **Renouf**, Prof. L. P. W.; University College, Cork, Eire.
A. **Reynoldson**, T. B., Ph.D.; Dept. of Zoology, University College of North Wales, Bangor, N. Wales.
E. **Rhodes**, Prof. A. D.; Forestry Dept., Massachusetts State College, Amherst, Mass., U.S.A.
A. **Ribbands**, C. R., M.A.; Rothamsted Experimental Station, Harpenden, Herts.
E. **Ribbons**, B. W.; 28 Boundary Road, Norwich, Norfolk.
E. A. **Richards**, O. W., M.A., D.Sc.; Zoology Dept., Imperial College of Science, S. Kensington, London, S.W. 7.
E. **Richards**, P. T.; New College, Oxford.

E. **Richards**, Prof. P. W., M.A., Ph.D.; Dept. of Botany, University College, Bangor.
E. **Richards**, Mrs S. A., M.A.; Coed Menai, Upper Bangor, Caern.
A. **Richards**, Dr W. S.; c/o M.C.P.S., Wad El Hur, Anglo-Egyptian Sudan.
A. **Richdale**, L. E.; 23 Skibo Street, Kew, Dunedin, New Zealand.
A. **Rintoul**, Miss L. J.; Balsusney, Upper Largo, Fife.
A. **Roberts**, B. B.; Scott Polar Research Institute, Lensfield Road, Cambridge.
A. **Roberts**, H., B.Sc.; South Stoneham House, Swaythling, Southampton.
E. **Roberts**, H. A., B.Sc.; Strebor, Springfield Road, Ulverston, Lancs.
E. **Roberts**, Prof. R. Alun; Agricultural Dept., University College, Bangor, N. Wales.
E. **Robertson**, A. G., B.Sc.; 2 Westfield Park, Bristol 6.
E. **Robertson**, D. A., B.Sc.; 45 St George's Road, Cullercoats, Northumberland.
E. **Robertson**, Miss E. T., B.Sc., F.G.S.; Dept. of Botany, The University, Old Aberdeen.
E. **Robertson**, R. N.; The Botany Dept., The University, Sydney, Australia.
E. **Rorison**, I. H.; 32 Wansunt Road, Bexley, Kent.
E. **Rosayro**, R. A. de, B.A., B.Sc.; Forest Dept., P.O. Box 500, Colombo, Ceylon.
E. **Rose**, F.; The Forge House, East Malling, Maidstone, Kent.
Rosenberg, Dr Marie (Mrs Burton); *see under* Dr M. B. Burton.
E. **Ross**, R., B.A.; British Museum (Nat. Hist.), Cromwell Road, London, S.W. 7.
A. **Rothschild**, The Hon. Miriam; Ashton Wold, Peterborough.
E. **Round**, F. E., B.Sc.; Botany Dept., The University, Edgbaston, Birmingham 15.
E. A. **Rowntree**, J. R. B., M.A.; Hilla Green Farm, Hackness, Scarborough, Yorks.
E. **Rübel**, Dr E.; Zürichbergstrasse 38, Zürich 44, Switzerland.
E. **Russell**, Dr E. W.; Dept. of Agriculture, Parks Road, Oxford.
E. **Russell**, Dr R. S.; Dept. of Agriculture, Parks Road, Oxford.
E. **Russell-Wells**, Miss B., Ph.D.; Biology Dept., Lancing College, Shoreham, Sussex.
E. **Rutter**, Dr A. J.; Botany Dept., Imperial College of Science, S. Kensington, London, S.W. 7.
A. **Rzóska**, Julian R. D.; Gordon Memorial College, Khartoum, A.-E. Sudan.
E. A. **Sale**, G. N., B.Sc.; The Nature Conservancy, 83–91 Victoria Street, London, S.W. 1.
E. **Salisbury**, Sir Edward J., C.B.E., D.Sc., F.R.S.; Royal Botanic Gardens, Kew, Surrey.
A. **Salt**, G., D.Sc., Sc.D.; King's College, Cambridge.
A. **Sandison**, Miss E. E., B.Sc.; Dept. of Zoology, West Mains Road, Edinburgh 9.
E. **Sangster**, R. G.; Assistant Conservator of Forests, P.O. Box 31, Entebbe, Uganda.
A. **Sankey**, J. H. P., B.Sc.; Juniper Hall Field Centre, Dorking, Surrey.
E. **Sansom**, Miss J. M., B.Sc.; 149 Sandbanks Road, Parkstone, Dorset.
E. **Santapau**, Rev. H., Ph.D.; St Xavier's College, Cruikshank Road, Bombay 1, India.
E. **Sappa**, Dr Francesco; Istituto Botanico, Viale Mattioli 31, Turin, Italy.
E. A. **Saunders**, J. T., M.A.; University College, Ibadan, Nigeria.
A. **Savage**, R. M.; Rosendaui, Parkgate Crescent, Hadley Wood, Barnet, Herts.
E. **Schelpe**, E. A. C. L. E., M.Sc.; Wadham College, Oxford.
E. **Scurfield**, G., Ph.D.; Botany Dept., Manchester University.
E. A. **Segadas-Vianna**, F., B.Sc.; Rua Rainha Guilhermina, 83 Leblon, Rio de Janeiro, Brazil.
E. **Shaw**, Miss M. S., B.Sc.; Woodlea, Honley, nr Huddersfield.
E. **Sheldon**, J., B.Sc.; 'Greystones', Bately Avenue, Gorleston-on-Sea, Norfolk.
A. **Shelford**, Prof. Victor E.; Vivarium Building, Wright and Healey Streets, Champaign, Ill., U.S.A.
E. **Sherrin**, W. R.; South London Bot. Inst., 323 Norwood Road, Herne Hill, London, S.E. 24.
E. **Sherwood**, E. G. P., M.A.; c/o I.C.I. Ltd., 12 Upper Belgrave Street, London, S.W. 1.
E. **Simmonds**, N. W., M.A.; Imperial College of Tropical Agriculture, St Augustine, Trinidad, B.W.I.
E. **Simpson**, N. Douglas, M.A., F.L.S.; 3 Cavendish Road, Bournemouth, Hants.
E. **Singh**, B. N., D.Sc.; Institute of Crop Physiology, 1 A Sultanpur Road, Lucknow, India.
A. **Singh**, C. P., B.Sc., M.Sc.; Zoology Dept. University College, Southampton.
E. A. **Skellam**, J. G., M.A.; 30 The Little Boltons, S. Kensington, London, S.W. 10.
E. **Skene**, Prof. Macgregor, D.Sc.; The University, Bristol 8.
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E. **Smith**, A. H. V., B.Sc.; 96 Berkshire Gardens, Palmer's Green, London, N. 13.
E. **Smith**, P. M. (Miss), B.Sc.; Osmotherley, Bromsgrove, Worcs.

A. **Smith**, Dr R. F., M.S., Ph.D.; 112 Agriculture Hall, University of California, Berkeley 4, California, U.S.A.
A. **Smyly**, W. J. P., B.Sc.; The Ferry House, Far Sawrey, Ambleside, Westmorland.
E. A. **Smyth**, J. C., Ph.D.; Dept. of Zoology, West Mains Road, Edinburgh 9.
A. **Solomon**, M. E., M.Sc.; 50 Dolphin Road, Slough, Bucks.
A. **Southern**, H. N., B.A.; Bureau of Animal Population, Botanic Garden, High Street, Oxford.
A. **Southwood**, T. R. B., B.Sc., A.R.C.S.; Dept. of Entomology, Rothamsted Experimental Station, Harpenden, Herts.
E. **Sowter**, F. A.; 9 North Avenue, Leicester.
E. A. **Spence**, A. C., M.R.C.S., L.R.C.P.; 7 Selwood Terrace, Onslow Gardens, London, S.W. 7.
E. **Spence**, D. H. N., B.Sc.; Botany Dept., The University, Glasgow, W. 2.
E. **Spooner**, G. M., M.A., M.B.E.; Marine Biological Laboratory, Citadel Hill, Plymouth.
A. **Spooner**, Mrs G. M.; Fiveoaks, Crapstone, Yelverton.
E. **Sporne**, K. R., M.A., Ph.D.; The Botany School, Cambridge.
E. A. **Stamp**, Prof. L. Dudley; 93 Sloane Street, London, S.W. 1.
E. **Stanbury**, Miss F. A.; Plymouth and Devonport Technical College, Tavistock Road, Plymouth.
A. **Stephen**, Dr A. C.; Royal Scottish Museum, Edinburgh.
A. **Stephenson**, J. W., B.Sc.; Entomology Dept., Rothamsted Experimental Station, Harpenden, Herts.
E. **Stephenson**, Prof. T. A., D.Sc.; Dept. of Zoology, University College of Wales, Aberystwyth.
A. **Stephenson**, Prof. W.; Dept. of Zoology, University of Queensland, Brisbane, Australia.
E. **Stevens**, A. J., B.A.; 25 Wings Road, Upper Hale, Farnham, Surrey.
A. **Stevens**, D. M.; Dept. of Zoology, West Mains Road, Edinburgh 9.
E. **Stevenson**, Miss E. H.; 28 Foxcombe Road, Weston, Bath, Somerset.
E. **Stewart**, Dr R. R., M.A.; Gordon College, Rawalpindi, Pakistan.
E. **Stiles**, Prof. W., M.A., Sc.D., F.R.S.; 'Elsley Lodge', Tilehurst on Thames, Reading.
A. **Stower**, W. J., B.Sc.; British Museum (Nat. Hist.), Cromwell Road, London, S.W. 7.
E. A. **Streets**, R. J., M.A.; c/o Forestry Dept., Nicosia, Cyprus.
A. **Strickland**, A. H., M.A.; Plant Path. Lab., Ministry of Agriculture, Milton Road, Harpenden, Herts.
E. A. **Summerhayes**, V. S., B.Sc.; Royal Botanic Gardens, Kew, Surrey (*Hon. Treasurer*).
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E. **Suxena**, M. R., M.Sc.; Botany Dept., Osmania University, Hyderabad, Deccan, India.
A. **Svendsen**, J. A., B.Sc.; 7 Palatine View, Durham City.
E. **Swann**, E. L.; 282 Wootton Road, King's Lynn, Norfolk.
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A. **Taylor**, D. J., B.Sc.; Woodside, Usk, Monmouthshire.
E. **Taylor**, F. J., M.Sc.; Dept. of Botany, Queen Mary College, Mile End Road, London, E. 1.
E. **Taylor**, G., D.Sc.; British Museum (Nat. Hist.), Cromwell Road, London, S.W. 7.
E. **Taylor**, Miss J., M.Sc.; Herbarium, Royal Botanic Gardens, Kew, Surrey.
E. **Taylor**, Miss M. H., B.Sc.; Belmont Farm, Clarendon, nr Salisbury, Wilts.
E. **Tedd**, H. Griffith; Bottor Cottage, Hennock, Bovey Tracey, Devon.
A. **Tener**, J. S., M.A.; Bureau of Animal Population, Botanic Garden, High Street, Oxford.
A. **Tevis**, Lloyd P.; Box 1416, Carmel, California, U.S.A.
E. **Thoday**, Prof. D., M.A., Sc.D., F.R.S.; Botany Department, The University, Leeds, 2.
E. A. **Thomas**, A. K., B.Sc.; 2 Norwood Road, Shipley, Yorks.
E. **Thomas**, A. S., D.Sc.; Goodings Cottage, Woodland St Mary, Newbury.
A. **Thomas**, J. F., B.A.; 17 Belle Grove Terrace, Spital Tongues, Newcastle-on-Tyne 2.
E. **Thomas**, H. Hamshaw, M.B.E., Sc.D., F.R.S.; Botany School, Cambridge.
E. **Thomas**, Miss M. K., B.Sc.; 33 Centurion Drive, Meols, Cheshire.
A. **Thompson**, H. V., B.Sc.; Ministry of Agriculture and Fisheries, Hook Rise, Tolworth, Surbiton, Surrey.

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A. **Thomsen**, H. P., Ph.D., M.S.; R.H. 3, Box 406, Beloil, Wisconsin, U.S.A.
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A. **Tinbergen**, Dr L.; Zoologisch Laboratorium, Groningen, Holland.
E. **Tincker**, M. A. H., M.A., D.Sc.; Hort. Dept., North of Scotland College of Agric., 41½ Union Street, Aberdeen.
A. **Tjønneland**, A.; Zoologisk Laboratorium, The University, Bergen, Norway.
E. **Todd**, Miss M. A., M.Sc.; c/o Agent General for Victoria, Victoria House, Strand, London, W.C. 2.
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A. **Toschi**, Prof. A.; Laboratorio di Zoologia, Via S. Giacomo 9, Bologna, Italy.
E. A. **Trapnell**, C. G., B.A.; E. African Agric. & Forestry Res. Organ., P.O. Box 21, Kikuyu, Kenya.
E. **Troll**, Prof. C.; Geographical Dept., University of Bonn, Bonn, Germany.
E. A. **Tucker**, D. G., Ph.D.; 'Three Ways', 115 Clearmount Road, Rodwell, Weymouth, Dorset.
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A. **Turner**, Miss M. A.; 4 Orchard Gardens, Dunsford Road, Exeter.
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A. **Tutin**, Mrs T. G., Ph.D.; University College, Leicester.
E. **Tüxen**, Prof. Reinhold; Schinnaerlandsstr. 6, Stolzenau/W., Germany.
E. **Tyler-Smith**, M. A.; Strathallan, Broadway, Southbourne, Bournemouth.
A. **Uvarov**, B. P., C.M.G., D.Sc.; British Museum (Nat. Hist.), Cromwell Road, London, S.W. 7.
E. **Valentine**, Prof. D. H., Ph.D.; University Dept. of Botany, Science Laboratories, South Road, Durham.
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A. **Vickers**, G. G., M.Sc.; Zoology Dept., University College, Exeter.
A. **Vincent**, Miss M. H., B.Sc.; 71 Saddler Street, Durham.
A. **Vizoso**, Mrs M. R., B.A.; 11 Churchdale Court, Harvard Road, Chiswick, London, W. 4.
A. **Vogt**, W.; 501 Madison Avenue, New York 22, N.Y., U.S.A.
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A. **Wagge**, Miss L. E., B.Sc., Ph.D.; 192 Lichfield Court, Richmond.
E. **Walker**, D., B.Sc.; Clare College, Cambridge.
E. **Walker**, F. T., B.Sc.; Institute of Seaweed Research, Inveresk Gate, Musselburgh, Midlothian.
E. A. **Wallace**, T. J.; Goodmans, Furley, Membury, nr Axminster, Devon.
A. **Waloff**, Miss Nadejda, Ph.D.; Dept. of Zoology, Imperial College of Science, Prince Consort Road, London, S.W. 7.
E. **Walters**, S. M., B.A.; Botany School, Downing Street, Cambridge.
E. **Walton**, Prof. J.; Dept. of Botany, The University, Glasgow.
E. **Wanstall**, P. J.; 54 Matlock Road, Brighton 5, Sussex.

E. **Warburg**, E. F., M.A., Ph.D.; University Dept. of Botany, South Parks Road, Oxford.
A. **Ward**, J. D. U.; Rodhuish, Watchet, Somerset.
E. **Watkins**, G., B.Sc.; Dyffryn, 13 Glanyrafon Road, Sketty, Swansea.
A. **Watson**, J. S., B.A., D.S.I.R. Animal Ecology Section, Wellington, New Zealand.
E. **Watson**, W., D.Sc.; Cedene, Cheddon Road, Taunton, Somerset.
E. A. **Watson-Walker**, J., B.Sc.; 12 The Bowley, Diseworth, Derby.
E. A. **Watt**, A. S., Ph.D.; The Botany School, Cambridge.
E. A. **Watt**, Mrs W. Boyd; 'San Simeon', 52 Wimborne Road, Bournemouth.
E. A. **Watterson**, J. G., B.Sc.; Tsetse Survey and Reclamation Dept., Box 396, Arusha, Tanganyika Territory.
E. **Webb**, Prof. D. A., Ph.D.; School of Botany, Trinity College, Dublin, Eire.
E. A. **Weese**, Prof. A. O.; Dept. of Zoological Sciences, University of Oklahoma, Norman, Oklahoma, U.S.A.
A. **Werth**, Miss I.; Dept. of Zoology, The University, Leeds 2.
E. **West**, Dr Cyril; The Cowl House, Holt Wood, Aylesford, Kent.
E. **West**, R. G.; 34 Elwill Way, Beckenham, Kent.
E. A. **Wheatley**, A. R., B.Sc.; Greenacre, Orchard Way, Esher, Surrey.
E. **White**, D. S., B.Sc.; 286 Priests Lane, Shenfield, Brentwood, Essex.
E. **White**, F., B.A.; Imperial Forestry Institute, South Parks Road, Oxford.
A. **White**, Miss K. M., B.Sc., Ph.D.; Glastonbury, Boyn Hill Avenue, Maidenhead, Berks.
E. A. **White**, O. M.; 78 Eastdale Road, Nottingham.
A. **White**, P. H. F., M.A.; Science Schools, Harrow School, Harrow, Middlesex.
E. **Whitehead**, F. H., B.A.; University Dept. of Botany, South Parks Road, Oxford.
E. **Whitehouse**, H. L. K., M.A., Ph.D.; Botany School, Cambridge.
E. **Whyte**, Dr R. O.; c/o Plant Prod. Branch, F.A.O. Viale delle Terme di Caracalla, Rome, Italy.
E. **Wiehe**, P. O.; Dept. of Agriculture, Zomba, Nyasaland.
E. **Wilkins**, D. A., B.Sc.; Scottish Soc. for Research in Plant Breeding, Corstorphine, Edinburgh 12.
E. **Wilkins**, W. C., B.Sc.; 8 Banc-y-Felin, Carmarthen, Wales.
A. **Williams**, C. B., Sc.D.; Rothamsted Experimental Station, Harpenden, Herts. (*President*).
A. **Williams**, G., B.Sc.; Zoology Dept., The University, Reading.
E. **Williams**, O. G., B.Sc.; Ministry of Agriculture and Fisheries, Shardlow Hall, Shardlow, nr Derby.
Williams, R. D., B.Sc., Ph.D.; 92 Loxley Road, Stratford-upon-Avon, Warwicks. (*Associate Member*).
E. **Williams**, Mrs S. S., B.Sc.; Grassland Research Station, Drayton, Stratford-on-Avon, Warwicks.
E. **Williams**, W. T., Ph.D.; Botany Dept., The University, Southampton.
E. A. **Williamson**, M. H.; Fairfield, Pullen's Lane, Oxford.
E. **Wilson**, I. E., B.Sc.; 73 Greenburn Drive, Bucksburn, Aberdeenshire.
E. **Wilson**, J. M., M.A.; St John's College, Oxford.
E. **Wilson**, J. W., M.A., D.Phil.; Dept. of Botany, The University, Reading.
A. **Wilson**, Mrs P. M. W., M.A., D.Phil.; 7 Denmark Road, Reading.
E. **Wilson Mayne**, W., B.Sc.; Scientific Officer, Messrs Kanan Devans Hills Produce Co. Ltd., Munnar P.O., Travancore, India.
A. **Winterbottom**, J. M., Ph.D.; Box 150, Livingstone, N. Rhodesia.
E. **Wood**, G. H. S., M.A.; c/o Imperial Forestry Institute, South Parks Road, Oxford.
E. A. **Woodcock**, G. S., F.R.E.S.; Ivy House, Bishop's Hall, Brentwood, Essex.
E. **Woodhead**, Norman, M.Sc.; Dept. of Botany, University College, Bangor, N. Wales.
E. A. **Worden**, Prof. A. N., M.A., B.Sc.; Cromwell House, Huntingdon.
E. **Wright**, A. C. S.; D.S.I.R. Soil Bureau, Aotea Quay, Wellington, New Zealand.
E. **Wright**, Mrs B. I., B.Sc.; 'Ecclesfield', 176 Stockbridge Road, Winchester.
E. **Wright**, Dr F. R. Elliston; Braunton, N. Devon.
E. A. **Yapp**, W. B., M.A.; Dept. of Zoology, The University, Edgbaston, Birmingham 15.
E. **Zehetmayr**, J. W. L.; 28 Groathill Avenue, Edinburgh 4.
E. **Zinderen Bakker**, Dr E. M. van; University of the Orange Free State, Bloemfontein, S. Africa.
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